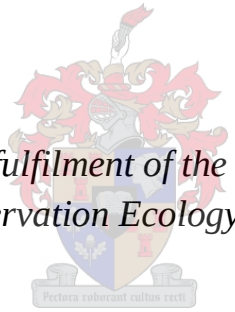
The response of biological communities to natural and anthropogenic habitat fragmentation in South Outeniqua Sandstone Fynbos, South Africa

by
Rory Nimmo Sandberg



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Supervisor: Professor Karen J. Esler
Co-Supervisor: Dr. Nicky Allsopp
Co-Supervisor: Professor William J. Bond
Faculty of AgriSciences
Department of Conservation Ecology & Entomology

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DECLARATION

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On the 27th of September 2013

ABSTRACT

Habitat fragmentation through the loss and modification of natural ecosystems poses a serious threat to biodiversity globally. Mechanisms and ecological implications of fragmentation have been extensively studied, yet new and meaningful insights continue to be produced. The highly diverse and ecologically complex fynbos shrubland communities that occur in the Cape Floristic Region of South Africa are amongst the most threatened by habitat fragmentation by urban, agricultural and silvicultural land uses and to the spread of invasive alien plants. Fynbos vegetation communities are fire-adapted and exploit the post-fire regeneration niche. Natural stochasticity in the fire regime means that these communities are temporally unstable; a factor that allows for the coexistence of such extreme diversity. Few studies have attempted to assess the influence of habitat fragmentation on this stochasticity, or to investigate the response of biological communities to the conditions that result. It is unknown whether this temporal instability will lead to delayed extinctions in fragmented communities, thus generating extinction debt. South Outeniqua Sandstone Fynbos occurs as a unique landscape mosaic of both insular and extensive habitats, suited to study through an island biogeography framework. Vegetation community stability was assessed through the comparison of historic and recent data sets. The responses of local vegetation and avifaunal communities to habitat fragmentation were assessed and compared on the basis of their differing motility. The unique habitat configurations also allowed for the investigation of extinction debt in the local communities and provided an opportunity to assess the influence of the surrounding matrix on species persistence and on connectivity in the artificial fragments. Data were analysed through simple regression analyses, modified Chi-squared tests and through ordination analyses. Ultimately the value of the artificial habitat fragments for the conservation of biological communities was assessed.

Stability was observed in the vegetation species-area relationship for the natural islands and the mainland sites over twenty-two years. Smaller islands were found to receive fewer fires than large islands and the mainland. This consistently over-extended fire-return interval reduces the stochasticity of the local fire regime causing stable yet depauperate vegetation communities to result. Vegetation communities in the artificial fragments were found to hold area-related extinction debt, possibly due to the relatively long-term demographic turnover that typically occurs in fynbos.

Avifaunal communities varied in their response to fragmentation relative to the vegetation. Birds – being motile – were found to be unaffected by isolation distance or surrounding matrix type – their response due more to changes experienced in the vegetation community than to geographic constraints. Fynbos-typical birds responded to the post-fire age of vegetation. Frugivorous birds and the matrix-habitat edge were identified as sources of alien and non-fynbos plant species that colonise the artificial fragments, potentially reducing the quality of these habitats for avifauna.

Fragmented communities of South Outeniqua Sandstone Fynbos have the potential to function as biological reserves. This potential can be realised through the implementation of a fire regime that acknowledges the stochasticity required by the vegetation, the frequency required by the vegetation and the avifauna, and the practicality required by surrounding anthropogenic land-uses.

OPSOMMING

Habitat-fragmentering, deur die verlies en verandering van natuurlike ekosisteme, hou 'n ernstige bedreiging in vir biodiversiteit wêreldwyd. Meganismes en ekologiese implikasies van die fragmentering is al breedvoerig bestudeer, maar nuwe en betekenisvolle insigte word voortaan vervaardig. Die hoogs diverse en ekologies komplekse fynbos-struikveld gemeenskappe wat in die Kaapse Floristiese Streek van Suid-Afrika voorkom, word meeste bedreig deur habitat-fragmentering deur verstedeliking, landbou en houtteeltkundige grondgebruike en die verspreiding van indringerplante. Fynbos gemeenskappe is aangepas tot vuur en die uitbuiting van post- vuur herlewing nis. Natuurlike stogastisiteit in die vuur-bedeling beteken dat hierdie gemeenskappe tydelik onstabiel word, 'n faktor wat die mede-bestaan van uiterste diversiteit moontlik maak. Min studies het al die invloed van habitat-fragmentering op hierdie stogastisiteit ondersoek, of die reaksie van biologiese-gemeenskappe tot die voortspruitende omstandighede. Dit is onbekend of die tydelike onstabiliteit sal lei tot vertraagde uitsterwing in gefragmenteerde gemeenskappe, dus genereer uitsterwings-skuld. Suid Outeniqua Sandsteen Fynbos kom as 'n unieke landskap mosaïek van beide die eilande en uitgebreide habitatte voor, geskik om deur 'n eiland biogeografie raamwerk bestudeer te word. Plant-gemeenskappe se stabiliteit is bestudeer deur die vergelyking van historiese en onlangse data stelle. Die reaksies van die plaaslike plantegroei en voëllewe gemeenskappe tot hul habitat is bestudeer en vergelyk op grond van hul verskillende beweeglikheid. Die unieke habitat konfigurasies het ook toegelaat vir die ondersoek van uitsterwings-skuld in die plaaslike gemeenskappe en 'n geleentheid gebied om die invloed van die omliggende habitat-matriks op spesies volharding en op konneksie in die kunsmatige fragmente te bepaal. Die data is ontleed deur middel van eenvoudige regressie analises, aangepasde Chi -kwadraat toetse en deur koördinerings ontledings. Ten einde die waarde van die kunsmatige habitat fragmente vir die bewaring van biologiese gemeenskappe te bepaal.

Stabiliteit in die plantspesies-area verhouding vir die natuurlike eilande en die vasteland van webwerwe oor twee en twintig jaar was waargeneem. Kleiner eilande het minder brande aangeneem as groot eilande en die vasteland. Hierdie herhaalde oor-uitbrei over-extended vuur-interval het die stogastisiteit verminder van die plaaslike vuur-bedeling wat stabiele tog spesie-arme plantegroei gemeenskappe veroorsaak het. Plantegroei gemeenskappe in die kunsmatige fragmente is bevind om spesie- area -verhouding uitsterwings-skuld te bevat, moontlik as gevolg van die relatiewe lang termyn demografiese omset wat tipies voorkom in fynbos.

Voëllewe gemeenskappe het gewissel in hul reaksie tot die fragmentering relatief tot die plantegroei. Voëls – weens hul beweeglikheid – blyk om nie beinvloed te word deur isolasie afstand of omliggende habitat-matriks tipe nie - hul reaksie blyk meer asgevolg van veranderinge wat ervaar word in die plantegroei gemeenskap as geografiese beperkinge. Fynbos-tipiese voëls reageer op die post- vuur ouderdom van plantegroei. Vrugte-etende voëls en die habitat-matriks rand is geïdentifiseer as bronne van uitheemse en nie-fynbos plantspesies wat die kunsmatige fragmente koloniseer, wat potensieel die kwaliteit van hierdie habitatte vir voëls verminder.

Gefragmenteerde gemeenskappe van Suid Outeniqua Sandsteen Fynbos het die potensiaal om as biologiese reserwes te funksioneer. Hierdie potensiaal kan verwesenlik word deur die implementering van 'n vuur-bedeling wat erkenning verleen aan die stogastiesiteit vereis deur die plantegroei, die frekwensie wat deur die plantegroei en die voëllewe vereis word , en die praktiese vereistes van die omliggende menslike grondgebruike.

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I would like to thank the Lord for His provision and strength, and for his guidance from the initial stages of this project to its completion, "*What has been will be again, what has been done will be done again; there is nothing new under the sun*" – Ecclesiastes 1 v 9.

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CHAPTER 1 - GENERAL INTRODUCTION

1.1. INTRODUCTION

The fragmentation of natural habitat has been identified as a major global threat to biodiversity, particularly in fast developing areas (Saunders et al., 1991; Sala et al., 2000). In many aspects, habitat fragments resemble islands which have been used as a model framework through which to study and understand ecological processes that occur in fragment communities (Pickett & Thompson, 1978; Laurance, 2008). Habitat fragmentation occurs when human land-uses modify natural habitat, leaving a mosaic of variously sized and isolated habitat patches embedded in a land-use matrix (Wilcox, 1980; Wilcox & Murphy, 1985; Saunders et al., 1991; Sisk et al., 1997; Dunford & Freemark, 2004). Habitat loss to anthropogenic land uses, together with the spread of invasive alien plants into natural state habitats, is a major driver of change in the Cape Floristic Region of South Africa (Rouget et al., 2003).

Fragmented communities generally show some level of response to reduced habitat area and increased isolation by the human modified matrix that surrounds them (Saunders et al., 1991; Andrén, 1994; Fahrig, 2003), however, this is dependent on the nature of the species or community (Henle et al., 2004) and on the amount of time elapsed since the fragmentation event (Tilman et al., 1994; Malanson, 2008). Island biogeography theory recognises habitat area and isolation as the two dominant constraints that affect rates of local immigration and extinction in island communities and thus govern the nature of the biological community that occupy an island at equilibrium (Preston, 1962; MacArthur & Wilson, 1963, 1967; Saunders et al., 1991). Inferences can be made regarding these responses from the presence or absence of species at given habitats. Because of the parallels between natural fragments or islands and artificial fragments, ecologists have often turned to the field of island biogeography as a possible framework for understanding the events and processes that occur in habitat fragments and to which local biodiversity may respond (Diamond, 1975; Diamond et al., 1976; Pickett & Thompson, 1978; Faaborg, 1979, and see Chapter 2, Section 2.3). This study occurred in the Southern Cape of South Africa (part of the Cape Floristic Region) and was concerned with South Outeniqua Sandstone Fynbos (Rebelo et al., 2006) – a vegetation sub-unit with a documented history of connectivity and isolation; processes which shaped it into a unique landscape mosaic (Cameron, 1980; Bond et al., 1988; Midgley & Bond, 1990; Russell et al., 2009). The region has a temperate climate, receiving all-year rainfall of 872 mm per annum (Schulze, 1965; Kraaij et al., 2012b). The plateau's geology is composed of pre-Cape granite, Kaaiman Group sediments and Table Mountain sandstone (Phillips, 1931; Rebelo et al., 2006; Russell et al., 2009). Although these substrates determine which fynbos type may persist, substrate is not a limiting factor in the distribution of fynbos or forest in this region (van Daalen, 1981). South Outeniqua Sandstone Fynbos is characterised by tall, fire-prone shrubland occurring on south and north facing slopes to the south of the Outeniqua Mountain range (Rebelo et al., 2006). This vegetation sub-unit provides habitat to various fauna, including birds. As in all fynbos habitats, South Outeniqua Sandstone Fynbos vegetation relies on periodic fires and is adapted to a particular fire-return interval (Kruger & Bigalke, 1984; Keeley, 1986; Southey, 2009; Kraaij et al., 2012a, 2012b, 2013a). Lightning is the dominant natural source of these fires in fynbos but fires of human origin are also common (Southey, 2009; Kraaij et al., 2012a, 2012b). Plant-pollinator mutualisms between flowering fynbos plants and nectarivorous birds are ecologically important (Johnson, 1992; Bond, 1994; Pauw & Louw, 2012;

Chalmandrier et al., 2013). See Chapter 2, Section 4 regarding the details of fynbos community dynamics.

South Outeniqua Sandstone Fynbos occurs naturally as two habitat configuration types: extensive **'mainland' areas** and smaller, isolated **natural habitat 'islands'** that are surrounded by Southern-Afrotemperate Forest (Bond et al., 1988; Midgley & Bond, 1990; Mucina & Geldenhuys, 2006; Rebelo et al., 2006). The natural isolation of the islands occurred in the early Holocene when natural climate change towards hotter temperatures and increased rainfall (Scholtz, 1986) drove forest expansion into areas previously dominated by fynbos (Midgley & Bond, 1990; Mucina & Geldenhuys, 2006). The natural islands' persistence has been attributed to periodic fires that originate from lightning strike and from wind-blown cinders (Bond et al., 1988; Midgley & Bond, 1990; Geldenhuys, 1994). The island effects observed in the smaller islands are attributed to the altered fire regime (Bond et al., 1988). The natural fire return interval observed in mainland South Outeniqua Sandstone Fynbos areas is between eight and twenty-six years (Kraaij et al., 2012a, 2013b).

South Outeniqua Sandstone Fynbos vegetation is considered to be vulnerable, threatened by agriculture and plantation forestry (Rebelo et al., 2006). Over the past two centuries these land uses together with urban development have further fragmented sections of the remaining mainland areas resulting in an assortment of **'artificial' fragments**, differing in size, isolation and the nature of their surrounding matrix (Filmalter & O'Keeffe, 1997; Russell et al., 2009). These fragments are typically surrounded by a matrix of plantation forestry, agriculture, dense invasive alien vegetation, indigenous forest or a combination of these (Filmalter & O'Keeffe, 1997; Russell et al., 2009). Therefore natural and artificial processes have resulted in three main South Outeniqua Sandstone Fynbos habitat configurations: natural islands, mainland areas and artificial fragments. These terms will be used throughout this study. These habitats are largely protected by the Garden Route National Park (Figure 1.1) and three other conservation areas (Rebelo et al., 2006), but many of the artificial fragments are located on private land. In general, fynbos specialist and endemic bird species are not considered to be threatened, however this is currently under review (Keith et al., 2008; Huntley & Barnard, 2012; Lee & Barnard, 2012; Chalmandrier et al., 2013).

The various habitat configurations present an opportunity to investigate the effects of habitat fragmentation on biological communities that inhabit South Outeniqua Sandstone Fynbos. Empirical species richness data, together with available historic data regarding species richness, fire frequencies and isolation history allow for the stability of island species-area relationships over a 22 year period to be tested. Although it is likely that many historical natural islands have transformed to forest, those islands that are situated in the path of hot berg-winds, associated with wildfire spread (Kraaij et al., 2012b), receive fire frequently enough to persist as fynbos (Geldenhuys, 1994). Bond et al. (1988) found that a plant island species-area relationship exists on these islands, which they attributed to assumed area-based differences in the frequency of fire on the islands (see Chapter 3, Section 3.1); smaller islands present smaller targets for lightning strike or the wind spread of cinders.

When natural habitat becomes increasingly fragmented (Saunders et al., 1991; Sala et al., 2000) it is important to know how biological communities will respond and how best to manage this response. Some plants, such as trees and resprouters, have characteristically long life-spans (Kuussaari et al., 2009; Garcia et al., 2011; Hylander & Ehrlén, 2013) and vegetation communities often develop through long-term successional cycles or regeneration stages (Horn, 1975; Eriksson, 1996; Mergeay et al., 2007; Hylander & Ehrlén, 2013). Thus the response of plant communities to fragmentation may not be immediately apparent (Wiens, 1994; Ewers & Didham, 2006, and see Chapter 3). This delayed response is termed an extinction debt and it implies that certain species will go locally extinct at some

future time under the current fragment conditions (Tilman et al., 1994; Hanski & Ovaskainen, 2002; Malanson, 2008). Extinction debt has been found to persist for over a century in the vegetation of other ecosystems (Vellend et al., 2006). If the fynbos plant species-area relationship that was established by Bond et al. (1988) is found to be stable then it can be assumed to represent a new equilibrium level of species richness for natural fynbos islands (MacArthur & Wilson, 1963, 1967; Diamond, 1975). Following this, the presence of an extinction debt in the artificial fragment vegetation can be investigated and quantified (see Chapter 3).

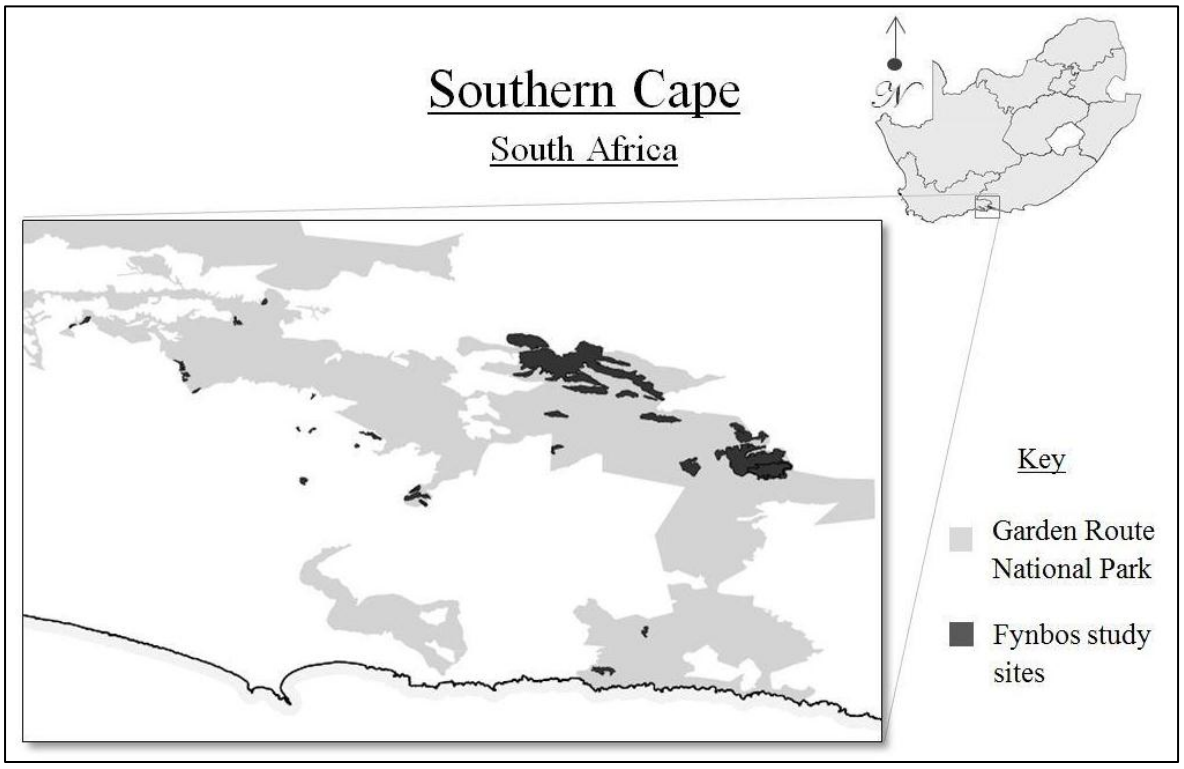

Figure 1.1. Map of the study area, illustrating the fynbos study sites and some of the Garden Route National Park in the Southern Cape.

Bird communities that inhabit South Outeniqua Sandstone Fynbos have received little attention in the form of ecological research. Although fynbos-typical avifauna is less diverse than fynbos vegetation, a number of ecologically important endemic bird species occur in South Outeniqua Sandstone Fynbos habitats, including the Cape Sugarbird (*Promerops cafer*) and the Orange-breasted Sunbird (*Anthobaphes violacea*), (Hockey et al., 2005); both are pollinators of fynbos vegetation (Bond, 1994; Pauw & Louw, 2012; Chalmandrier et al., 2013). Being nectarivores, these birds are dependent on the availability of mature, flowering plants, leaving them sensitive to the post-fire age of vegetation (Chalmandrier et al., 2013). Habitat fragmentation can disrupt natural fire regimes and therefore may impact avifaunal communities though these changes. The various fragment sizes, degrees of isolation and the nature of their surrounding matrixes (Cameron, 1980; Bond et al., 1988; Filmalter & O'Keeffe, 1997; Russell et al., 2009) may influence the respo

nse of bird communities. Because birds are motile it is likely that their response to these constraints differs to that of sedentary plant communities which cannot migrate. If the fire-return interval does indeed vary between differently sized fynbos patches then it could also be an important factor in determining the response of fynbos-typical avifauna to habitat fragmentation (see Chapter 4). The natural islands present something of a model framework, free from extinction debt or diverse matrix

effects, with which to investigate avifaunal response to fragmentation. Because birds are pollinators and dispersers (Bond, 1994; Pauw & Louw, 2012; Chalmandrier et al., 2013) of isolated plant species, this response has likely ecological consequences.

1.2. STUDY OBJECTIVES AND CHAPTER AIMS

The objective of this study is to assess the various responses of biological communities to habitat fragmentation in South Outeniqua Sandstone Fynbos in order that their conservation may be efficiently managed. I focus on vegetation and avifauna to investigate the role of motility and community development patterns in shaping a particular response.

Through this thesis I aim to:

- Chapter one:
  - Introduce the overall study, its objectives and its geographic and investigative extent;
- Chapter two:
  - Review the published literature regarding the historic developments that have led to the current understanding of fragmented communities and their responses;
- Chapter three:
  - Examine the effect of patch area on fire-return interval in fynbos vegetation;
  - Investigate the relative stability of natural island vegetation communities over a 22 year period;
  - Assess the response of vegetation communities to artificial fragmentation with particular focus on the response to patch area;
  - Investigate and quantify the presence of extinction debt in the artificial fragment plant communities and species groups by comparing them to those in the natural islands;
- Chapter four:
  - Investigate species-area relationships in the avifauna of three habitat configurations relative to those in the vegetation communities;
  - Assess the association between avifaunal migratory groups and artificial fragment connectivity – measured as isolation distance and the nature of the surrounding matrix;
  - Examine the pathways through which matrix-typical vegetation, capable of lowering bird habitat quality, enters artificial fragments;
  - Investigate the response of fynbos-typical avifauna to post-fire vegetation age.
- Chapter five:
  - Discuss the results of previous chapters in relation to the published literature
  - Develop conservation management recommendations regarding the study subjects and the study area.

1.3. RESEARCH APPROACH

In this *Chapter 1*, an introduction to the study is given. The study's goals, its rationale and the procedures through which it will be conducted are introduced in this chapter. It serves as a reference to all that is to follow in subsequent chapters.

Chapter 2 reviews the scientific literature concerned with habitat fragmentation. The review gives special attention to the historic developments in the field of equilibrium island biogeography that have led to the current understanding of insular habitats. Addressed are topics including motility, life span, successional and regeneration cycles and interdependence of taxa. These are viewed against the many individual pressures that are known to affect fragmented communities. Ultimately the review will compile the current knowledge of the pressures that must be managed in the conservation of fragmented communities and present insights into the effectiveness of various management tools that have been developed. In doing so, this chapter aligns the study with the scientific literature and provides the rationale for its completion.

The literature associated with fragmentation and the theory of island biogeography has been generated over a broad time scale, and therefore an extensive literature review will not be restricted to the recently published literature.

The first data chapter, *Chapter 3*, uses historic data together with recently collected data to validate the temporal stability of the species-area relationship – discovered by Bond et al. (1988) – in the natural islands and in the mainland. The chapter goes on to assess the species and growth form richness of the artificial fragments, and to investigate the hypothesised presence of extinction debt. This chapter deals exclusively with vegetation data. The importance of identifying extinction debt in the vegetation community when selecting fragment patches for biodiversity reserves is addressed.

Chapter 4 assesses the value of fynbos fragments for the conservation of avifauna. Recent data concerning both the vegetation and the avifaunal community is used to investigate which fragmentation-related factors inhibit the use of artificial fragments by fynbos-typical avian species. This chapter provides insights into the use of fragments as 'stepping-stones' and resource refugia by birds.

The final chapter, *Chapter 5*, is an integrative discussion that combines the findings of previous chapters and discusses them relative to the scientific literature. Here the overarching study goals are addressed and novel insights are made. Rationale for future scientific research and for development of management prescriptions can be drawn from this chapter.

The dual purpose of this thesis is to generate scientific knowledge and to disseminate appropriate guidance to conservation ecologists. Therefore it has been written as a series of scientific papers. Each chapter functions as a stand-alone piece; however cross-referencing has been used to facilitate reading and to minimise repetition between chapters.

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CHAPTER 2: LITERATURE REVIEW - COMMUNITY RESPONSE TO HABITAT FRAGMENTATION: LOOKING TO A HERITAGE OF ISLAND BIODIVERSITY FOR DIRECTION

2.1 INTRODUCTION

The fragmentation of natural habitats is a threat that faces biological communities globally, and is predicted to become more prominent in the future (Saunders et al., 1991; Sala et al., 2000; Foley et al., 2005). Understanding the manner in which species or communities respond to the physical changes associated with habitat fragmentation is vital if effective conservation strategies are to be developed (Fahrig & Merriam, 1994; Laurance, 2008; Martensen et al., 2008). This understanding should acknowledge the four main aspects of habitat fragmentation: reduced patch area, increased isolation, increased modification of the surrounding matrix (Ricketts, 2001; Jules & Shahani, 2003; Murphy & Lovett-Doust, 2004) and the amount of time elapsed since isolation (Tilman et al., 1994; Malanson, 2008; Hylander & Ehrlén, 2013). The variability of species response to these aspects makes this understanding complicated, especially in communities that are characterised by non-linear interactions, such as fynbos vegetation communities (Bond et al., 1992; Thuiller et al., 2007).

Theories and models developed in the field of island biogeography have been applied in the study of fragmented communities (Cook et al., 2002). Habitat fragments resemble islands to some degree (Faaborg, 1979; Cook et al., 2002) but there are also many differences, mostly regarding surrounding land-uses (Wiens, 1994) and the generally shorter time since isolation of fragments. Island biogeography has helped in part to understand the response of fragment communities (Haila, 2002; Laurance, 2008); however, no single general theory has successfully addressed the full complexity of all fragment systems. It is clear that the ultimate loss of species to fragmentation has yet to be reached in many situations which, although seemingly ominous, does provide hope for the potential of mitigation efforts. Through this review I investigate the current understanding of fragmented communities, natural and artificial, and use this understanding as rationale for the study approach that I have used to answer questions (see Chapter 1, Section 2 and 3) about fragmented South Outeniqua Sandstone Fynbos communities (Rebelo et al., 2006).

2.2 FROM THE THEORY OF ISLAND BIOGEOGRAPHY TO THE SCIENCE OF FRAGMENTATION

Island habitats have intrigued ecologists for over a century and have played an important role in the development of the evolutionary and ecological understanding that we have today. It is unlikely that the discoveries made by Charles Darwin (1839, 1859, 1860) and Alfred Russel Wallace (1869, 1876, 1881) on evolution and natural selection came coincidently following their exploratory trips to the Galapagos and the Malay Archipelagos respectively (Lomolino & Brown, 2009). MacArthur and Wilson (1967) highlighted “the importance of islands” in the first chapter of their book which went on to revolutionise the general understanding of landscape ecology at the time. Their book also founded the field of island biogeography theory which rapidly gained momentum and continues to inform ecologists today.

2.2.1 Islands by definition

By MacArthur and Wilson's (1967) description, islands are defined as insular habitats. Other authors distinguish between various kinds of islands. Oceanic islands – areas of land surrounded by sea – are the most simplistic form of island. Their binary nature of habitable land surrounded by non-habitable sea makes them suited to natural experiments (MacArthur & Wilson, 1967) and is the reason that they were used as the testing grounds for most of the early literature on island biogeography (MacArthur & Wilson, 1963, 1967; e.g. Diamond, 1969, 1972; Whitehead & Jones, 1969). Land-bridge islands typically vary between states of isolation and connection to the mainland or to other islands. They have also been defined as islands that were once connected to the mainland but became isolated through an inundation event (Diamond, 1972, 1975; Terborgh et al., 2001). Habitat islands are defined according to their isolation by some contrasting matrix that surrounds them. It seems somewhat abstract to describe these habitats as islands considering that they are surrounded by a landscape and not a seascape or water body. Instead they must be considered as functional islands, whereby certain taxa are effectively isolated and others free to move in and out. Isolated mountain ranges (Brown, 1971), streams (Angermeier & Schlosser, 1989; Taylor, 1997), caves (Culver, 1970; Vuilleumier, 1973; Brunet & Medellín, 2001), fire refugia, such as those used in this study (Bond et al., 1988; Midgley & Bond, 1990; Luger & Moll, 1993; Geldenhuys, 1994; Bowman, 2000), edaphic isolates (Ellis & Weis, 2006; Ellis et al., 2006) and even individual plants (Janzen, 1968, 1973; Opier, 1974; Seifert, 1975) and cattle droppings (Mohr, 1943; Curry, 1979) have been studied as habitat islands (see Chapter 3).

2.2.2 Equilibrium island biogeography

The focused study of insular habitats was catalysed by the revolutionary works of MacArthur and Wilson (e.g. MacArthur & Wilson, 1963, 1967). The field of island biogeography theory grew as scientists tested the predictions that they made in their theory under diverse conditions and with respect to various types of island (Laurance, 2008; Lomolino & Brown, 2009). The theory of island biogeography was also instrumental in exposing the threat posed by habitat fragmentation to biological communities (Laurance, 2008). In many cases the theory was found to be flawed in its application to complex island systems due to its idealistic, binary consideration of habitat surrounded by non-habitat (Brown, 1971; Diamond, 1972; Barbour & Brown, 1974; Heaney, 1986; Brown & Lomolino, 2000). This is attributed to its origins in simple oceanic island systems. Despite these flaws, island biogeography theory remains a useful framework through which to analyse aspects of the more complex ecological patterns that exist in insular habitats (Ward & Blaustein, 1994; Lomolino, 2000; Anderson & Wait, 2001; Blackburn et al., 2008; Diver, 2008).

The theory of island biogeography and its various 'amendments' generally predict that the rates of species extinction and immigration to an island are governed by the specific island area and distance by which the island is isolated from the mainland or another island. These rates of immigration and extinction thus result in an equilibrium level of species richness (Figure 2.1) unique to each island (Preston, 1962; MacArthur & Wilson, 1963, 1967). Thus it is likely that a change in the physical parameters of an island, such as area and isolation, will cause this equilibrium level to shift. Under uniform isolation, a network of increasingly large islands will display a positive (island) species-area relationship (Darlington, 1957; MacArthur & Wilson, 1963, 1967; Scheiner, 2003; Dengler, 2009). Bond et al. (1988) found that an island species-area relationship such as this exists in the vegetation community of the natural habitat islands that are used in this study. Therefore species-area relationships have been used to investigate the distribution of species in Chapters 3 and 4 of this study. Habitat area affects local biological communities on insular habitats in various ways

(Simberloff, 1976; Brunet & Medellín, 2001). Larger habitats will have more space to include a greater number of species than small habitats if species are distributed at random (Arrhenius, 1921; Coleman et al., 1982). Small habitats offer fewer resources than do large habitats and therefore they can only support smaller, less diverse communities (Williams, 1943; Connor & McCoy, 1979). These resources may include habitat niches (Kadmon & Allouche, 2007), foraging options and the potential to form ecological mutualisms (Inoue, 1993; Harris & Johnson, 2004) amongst others. One must consider that the size of an insular habitat will often be related to the habitat diversity therein. In the case of small oceanic islands for example, most of the habitat area will be strand-typical (of a coastal or beach nature) which limits the local community to include only strand-tolerant species (Whitehead & Jones, 1969). Larger insular habitats can also generally support greater species abundance than smaller habitats which equates to fewer density-dependent species extinctions and thus higher species richness at equilibrium (MacArthur & Wilson, 1963).

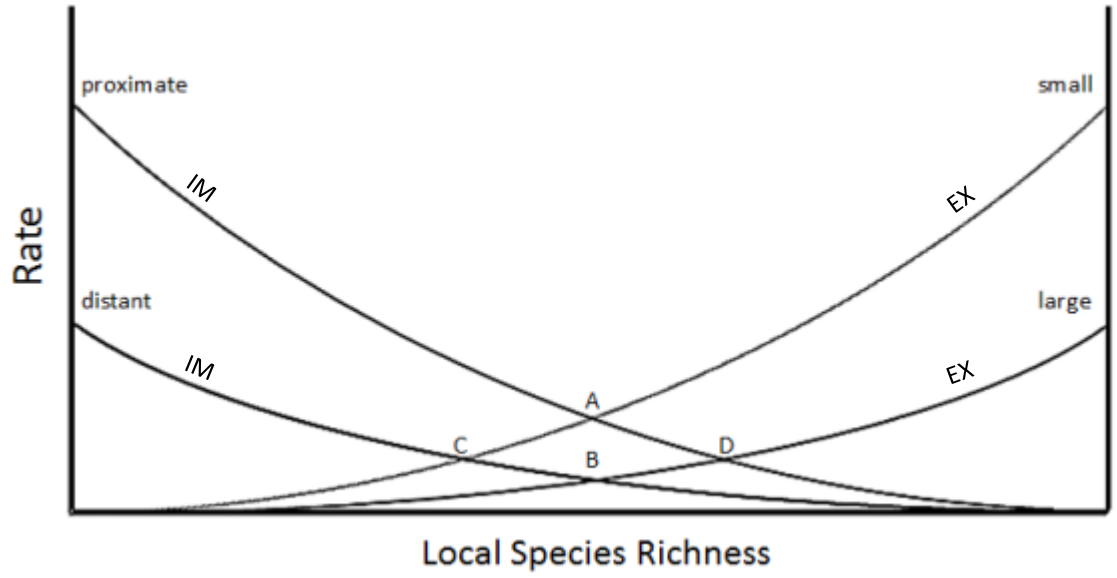

Figure 2.1. Equilibrium model of biodiversity on four hypothetical islands with varying levels of size and isolation. 'Rate' refers to the local rate of species immigration (IM) and species extinction (EX). A separate rate is shown for each of two isolation levels – 'proximate' and 'distant' and for each of two island sizes – 'small' and 'large'. The combination of these four hypothetical rates results in four possible equilibrium species levels: 'A' – for small, proximate islands; 'B' – for large, distant islands; 'C' – for small, distant islands; 'D' – for large, proximate islands (Adapted from MacArthur & Wilson, 1963).

The degree of isolation largely governs the rate of immigration to insular habitats (MacArthur & Wilson, 1963, 1967; Diver, 2008). For oceanic islands that are surrounded by an uninhabitable seascape, more distant islands will receive fewer colonists than more proximate islands. This is especially applicable when the existence of an island and the extent of its isolation are known to potential colonists and their migration to a more proximate island is the result of a calculated choice (Lomolino, 1990). The likelihood of 'passive' colonists reaching an island as the result of random drift is governed more by the size of the island than by its isolation: small islands present smaller targets to drifting colonists than do large islands – all other factors being equal (Whitehead & Jones, 1969; Lomolino, 1990). The rate of immigration also plays a role in the rate of local species extinction in small, insular habitats through what is termed the 'rescue effect' (Brown & Kodric-Brown, 1977). Marginal species populations that exist in these habitats can be sustained through re-colonisation events.

The state of dynamic equilibrium that is predicted by island biogeography theory (Preston, 1962; MacArthur & Wilson, 1963, 1967) to exist in an insular habitat will represent the species turnover that occurs in the habitat. Although ecological systems in dynamic equilibrium have been found to exist (Dickerson & Robinson, 1985) and this prediction has been defended by many scientists (Terborgh, 1974; Wilson & Willis, 1975; Diamond et al., 1976), it has also been extensively criticised, tested and rejected by many (Simberloff & Abele, 1976; Gilbert, 1980; Boecklen & Gotelli, 1984; Boecklen & Simberloff, 1986; Heaney, 2000). Critics argue that equilibrium theory of island biogeography fails to consider phylogenesis that may occur in local communities, the effect of varying habitat conditions (Heaney, 2000) and, in the case of habitat islands, the effect of heterogeneity in the surrounding matrix (Laurance, 2008), (e.g. Doak et al., 1992; Thomas et al., 1992). The theory also fails to account for systems that are absolutely isolated and in which extinction but no immigration occurs (Brown, 1971; Bond et al., 1988). Bond et al. (1988) found the fynbos vegetation on the natural islands to be isolated in this way – no seed dispersal across the surrounding Southern-Afrotemperate Forest (Mucina & Geldenhuys, 2006) matrix was apparent (see Chapter 3).

Through its various shortfalls, island biogeography theory has led scientists to establish new theories and models. The development of the metapopulation model for single species distribution (Levins, 1969; Hanski & Gilpin, 1991; Wiens, 1997; Moilanen & Hanski, 1998; Malanson, 2008) came soon after the island biogeography theory. This model looks at the competitive and dispersal abilities of individual species in order to describe their distribution between various ‘source’ and ‘sink’ habitats. The development of unified neutral theory (Hubbell, 2001) used island biogeography theory as a foundation. A major field of interest involved the application of equilibrium island biogeography theory to certain biological conservation issues, such as optimisation of reserve selection (Diamond, 1975; Diamond & May, 1981; Cowling & Bond, 1991; Ovaskainen, 2002) and investigating the effects of habitat fragmentation on communities (Faaborg, 1979; Haila, 2002; Laurance, 2008). Many authors have tried to use equilibrium theory to determine the minimum habitat requirements of isolated communities for the purpose of selecting protected areas and reserve networks for conservation (Diamond, 1975; Diamond & May, 1981; Cowling & Bond, 1991; Ovaskainen, 2002). Again, this approach has at times been met with criticism (Diamond et al., 1976; Simberloff & Abele, 1976; Abele & Connor, 1979) but has successfully provided a framework through which to start investigating these conservation questions (Haila, 2002; Laurance, 2008). Despite its faults, the equilibrium theory of island biogeography has provided the platform needed for the development of contemporary frameworks such as the metapopulation model and continues to inform scientists in fields of conservation.

2.2.3 Fragmentation, reserve selection and the ‘SLOSS’ debate

The definition of habitat fragmentation has been debated through the literature (Bunnell, 1999; Fahrig, 2003; Fischer & Lindenmayer, 2007; St-Laurent et al., 2009) and its use in many studies has been ambiguous. Habitat fragments are often more complex systems than natural islands and fragment communities respond to a variety of fragment effects (Andrén, 1994; Fahrig, 2003; Lindenmayer & Fischer, 2006; Fischer & Lindenmayer, 2007; Laurance, 2008). In some cases island biogeography theory has been successfully used to investigate the effects of habitat fragmentation (Laurance, 2008), yet the theory has proved too simplistic to address the complexity of all fragment systems (Ewers & Didham, 2006; Laurance, 2008). In defining habitat fragmentation, some authors have stressed the importance of distinguishing habitat loss from habitat fragmentation (Fahrig, 2003). This said, habitat fragmentation can only occur if a certain amount of habitat has already been lost (Fahrig, 2003). Other authors consider habitat loss to be one of the main aspects of habitat fragmentation along with reduced habitat fragment size and increased fragment isolation (Wilcox, 1980; Burgess & Sharpe,

1981; Wilcox & Murphy, 1985; Andrén, 1994; Drinnan, 2005). These geographical parameters resonate with those assumed in island biogeography theory (Preston, 1962; MacArthur & Wilson, 1963, 1967). This is the reason why so many studies of fragmented communities and reserve networks – which are ultimately fragmented systems (Newmark, 1996; Boone & Hobbs, 2004; Hayward & Kerley, 2009) – have turned to island biogeography theory for direction (MacArthur & Wilson, 1967; Diamond & May, 1981; Harris, 1984; Andrén, 1994; Haila, 2002; Laurance, 2008). Indeed, many studies have found that biological communities respond primarily to the area constraint of a fragment, as predicted by island biogeography theory, before the various fragmentation aspects that are not explained by the theory (Bender et al., 1998; Lee et al., 2002; Ferraz et al., 2007; Sekercioglu, 2007; Kieck, 2009).

Habitat islands, as discussed previously, are often formed through a process of natural fragmentation, induced by events such as climatic shifts, inundation events and edaphic or geological changes (Midgley & Bond, 1990; Watson, 2002; Ewers & Didham, 2006). The natural islands that are used in this study provide an example. Ecological systems that are fragmented by human land-use often respond to a far larger and more complex set of pressures and fragment attributes (Ewers & Didham, 2006). Fragments such as these are characterized by different patch sizes, shapes, levels of isolation and levels of contrast with the surroundings (Wilcox, 1980; Wilcox & Murphy, 1985; Wilcove et al., 1986; Saunders et al., 1991; Andrén, 1994; Sala et al., 2000; Flather & Bevers, 2002). These fragmentation components modify the physical effect of the microclimate within each patch (Saunders et al., 1991). Coupled with this fragmentation is the breakdown of certain ecological drivers, such as the correct fire regime (Bond et al., 1988; Saunders et al., 1991), ecological mutualisms and dispersal (Fahrig, 2003). These physical and biogeographical components drive change in the pattern of biotic communities living on fragment patches (Saunders et al., 1991).

Debate over the use of natural islands and island biogeography theory in fields of conservation science – notably reserve selection and fragmentation sciences – was captured under the "single-large or several-small" (SLOSS) question (Burkey, 1989; Baz & Garcia-Boyero, 1996; Ovaskainen, 2002; Laurance, 2008). Various authors advocated the use of island biogeography theory in reserve selection (Terborgh, 1974; Diamond, 1975; May, 1975; Wilson & Willis, 1975). Diamond (1975) proposed various reserve networks designed to optimise species persistence based on the assumptions of equilibrium theory. Simberloff and Abele (1976, 1982) opposed the view that reserve network design could learn from island biogeography theory on the basis that one large reserve may fail to include all of the spatial heterogeneity of the landscape: many small reserves may 'miss' some micro-habitats. It was also noted that dynamic equilibrium cannot be reached in such reserve networks due to delayed species turnover. Another prominent difference between natural islands and artificial fragments that island biogeography theory fails to acknowledge is the nature of the surrounding matrix (Cook et al., 2002; Laurance, 2008) and the effect that this matrix has on patch isolation or connectivity (Ricketts, 2001; Murphy & Lovett-Doust, 2004), the degree to which this matrix can support local insular biodiversity (Fahrig, 2001; Ricketts, 2001; Vandermeer & Carvajal, 2001), and the manner in which this matrix affects the quality of the fragment habitat (Janzen, 1983; Saunders et al., 1991; Stouffer & Bierregaard, 1995; Didham & Lawton, 1999; Laurance, 2008). Advocates of equilibrium theory in fragmentation science have assumed the matrix to be uninhabitable, analogous to the sea which surrounds oceanic islands (e.g. Doak et al., 1992; Thomas et al., 1992). In reality though, the matrix is of varying use and permeability to local fragment taxa (Gascon et al., 1999; Ricketts, 2001; Cook et al., 2002; Brotons et al., 2003).

Despite the evidence against the use of island biogeography theory in fragmentation science there is equal evidence for its use (e.g. Faaborg, 1979; Cook et al., 2002) provided that the documented

shortfalls and assumptions are acknowledged and controlled. Species motility and the species-specific permeability of the surrounding matrix can potentially facilitate the species turnover in habitat fragments that is required for reaching a state of dynamic equilibrium. This however remains to be tested. I have chosen to investigate the response of biological communities to fragmentation through the island biogeography framework. A unique opportunity is presented by the natural islands (see Chapter 1) in the chosen study area to investigate these responses while controlling for the matrix and edge effects that are typically associated with habitat fragments. This is done using vegetation data in Chapter 3 and avifaunal data in Chapter 4. These responses can then be compared to those observed in the artificial fragments (see Chapter 1) in order to investigate the various effects of fragmentation that are not addressed by the theory of island biogeography.

2.3 THE NATURE OF FRAGMENTATION

Habitat fragmentation is a major threat to biodiversity globally and fragmented ecosystems are becoming more common (Saunders et al., 1991; Sala et al., 2000). Even biodiversity reserves effectively resemble habitat fragments in a contrasting matrix of modified land (Newmark, 1996, 2008; Woodroffe & Ginsberg, 1998). Despite the complex definitions that have been derived for the process of fragmentation and the various documented pressures faced by fragmented communities, habitat fragments do resemble islands to some extent, but this is species dependent (Lee et al., 2002; Laurance, 2008). Many fragmentation studies still report large and dominating effects of fragment area (Bender et al., 1998; Lee et al., 2002; Ferraz et al., 2007; Kieck, 2009) and isolation (Lovejoy et al., 1984; Wilcove et al., 1986; Ferraz et al., 2007), although isolation is often more complex in fragments than in island systems and hence is studied as ‘connectivity’ (Merriam, 1984; Fahrig & Merriam, 1985; Taylor et al., 1993). These geographical constraints impact fragment communities in various ways, as explained by island biogeography theory (Preston, 1962; MacArthur & Wilson, 1963, 1967). Two important features of habitat fragments that are not covered by island biogeography are the effect of the modified matrix that surrounds a fragment and the influence of isolation age, *viz.* the amount of time that has elapsed since an initial fragmentation event.

2.3.1 The surrounding matrix

The matrix that surrounds a habitat fragment differs from that of an oceanic island which is surrounded by water, and from that of a habitat island which is typically surrounded by another type of natural terrestrial habitat, such as the edaphically isolated plant communities found in South Africa’s Succulent Karoo (Ellis & Weis, 2006). Biological communities in habitat fragments that have been isolated by human land-uses often respond to matrix and edge pressures that are not common to equivalent natural insular systems. Specifically, anthropogenic matrix types vary in terms of their permeability to local species (Gascon et al., 1999; Ricketts, 2001; Brotons et al., 2003) and disturbances (Turner et al., 1989; Andrén, 1994; Hargrove et al., 2000), their ability to support local species persistence (Gascon et al., 1999; Norton et al., 2000; Brotons et al., 2003; Jules & Shahani, 2003) and the type of alien species (Gascon et al., 1999; Buckley et al., 2006), novel disturbances and edge effects (Laurance & Yensen, 1991; Fagan et al., 1999; Mesquita et al., 1999; Ries et al., 2004; Tomimatsu & Ohara, 2004) that they introduce to a habitat fragment.

2.3.2 Matrix permeability

The permeability of a particular matrix type is also species dependent (Strayer et al., 2003). For example, an intensively managed plantation forestry matrix (‘B’ in Figure 2.2) may present a motile forest bird species with a higher level of permeability and hence a lower degree of isolation than it

would to an anemochorous forest plant species characterised by short distance seed dispersal. The plant species could eventually disperse across the matrix through subsequent generations, however the matrix would become an ecological trap (Woodward et al., 2001; Battin, 2004; Fischer & Lindenmayer, 2007) whereby forest propagules are removed by plantation management leaving little chance of successful migration. Thus the plant species is effectively isolated by the matrix (Ricketts, 2001). The forest bird however would perhaps choose not to migrate across an open matrix type, such as an agricultural field or fynbos shrubland habitat ('C' in Figure 2.2) due to the high level of contrast between these matrix types and the bird's forest habitat ('A' in Figure 2.2), (Brooks et al., 1999; Lindenmayer et al., 2002; Strayer et al., 2003). The plantation matrix may also be permeable to ornithochorous forest plants which can be dispersed across the low contrast matrix by forest bird vectors. Although this is a hypothetical example, situations such as this and various others may occur in the complex landscape mosaic that characterises the area of this study. These differences in matrix permeability are described by the dispersal hypothesis (Moilanen & Hanski, 1998; Pither & Taylor, 1998; Brotons et al., 2003). The indigenous forest that surrounds the natural fynbos islands is assumed to be effectively impermeable to the dispersal of fynbos vegetation species (Bond et al., 1988). Fynbos birds however may be able or willing to cross through or over the forest matrix. This is tested in Chapter 4. The various properties of different ecological boundary types, such as those found at the fragment-matrix interface, are discussed by Strayer et al. (2003). Their study yielded a system of boundary structure classification which is useful for understanding the nature of a given fragment/matrix interface.

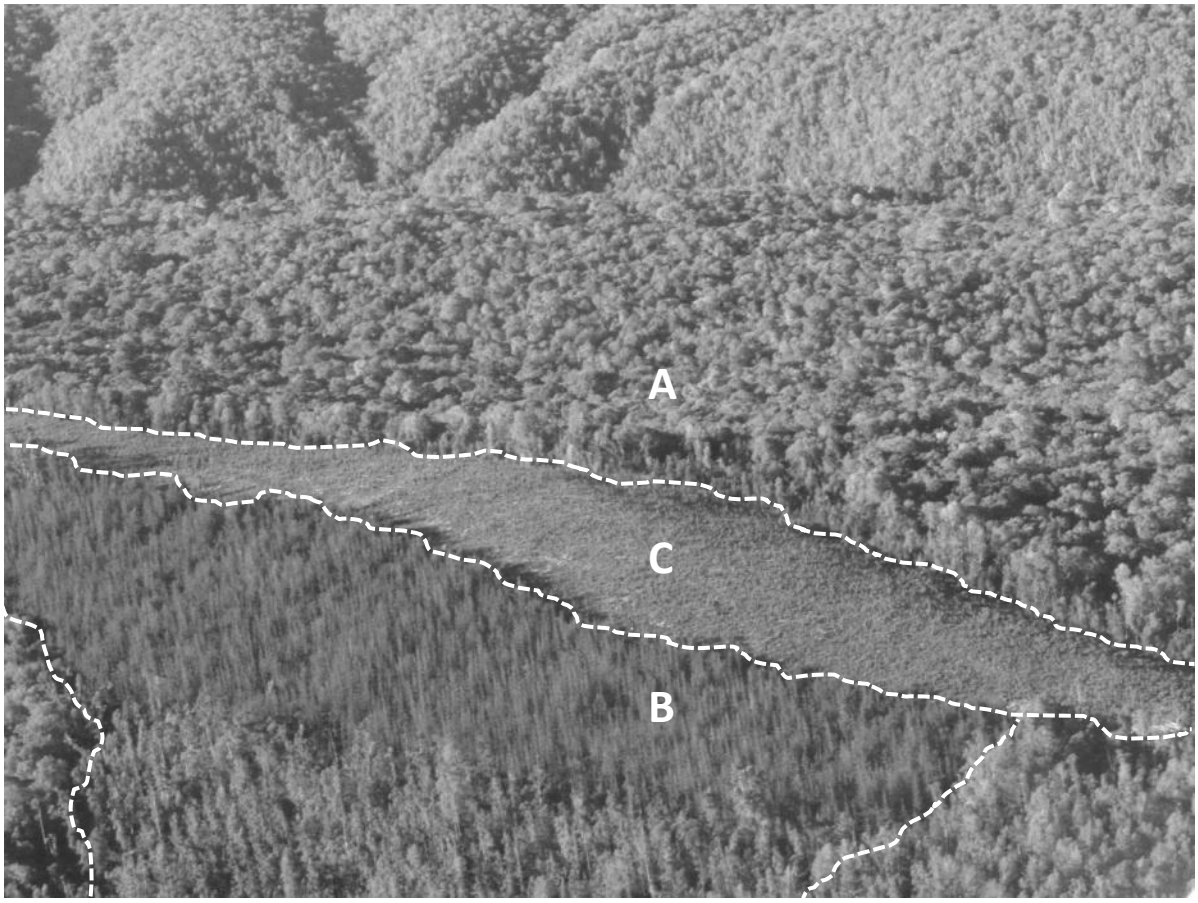

Figure 2.2. An example of contrasting habitat types which, when existing as a matrix, can vary in permeability and habitability for certain taxa. 'A' represents natural forest, 'B' represents intensively managed plantations and 'C' represents an open habitat type; fynbos shrubland in this case.

2.3.3 Effective area

Additionally to connectivity, the nature of the surrounding matrix can alter the area constraint of a habitat fragment for certain species (Gascon et al., 1999; Brotons et al., 2003; Jules & Shahani, 2003) as described by the habitat compensation hypothesis (Norton et al., 2000). Certain generalist species may be able to use matrix habitat for all of their requirements (Daily et al., 2001), including foraging and breeding. In this case their effective habitat area is larger than the physical area of the habitat fragment. Species that are more specialised may be able to use matrix habitat for individual aspects of their life-cycle, such as foraging, but not for all aspects. Successful breeding, for example, may be restricted to habitat fragments. Highly specialised species may not be able to use any aspect of the matrix habitat (Daily et al., 2001). For them the effective habitat area is equal to the size of the habitat fragment. Matrix habitat heterogeneity has also been found to increase the persistence of certain species in fragmented communities (Mayfield & Daily, 2005). This may be reflected through the species richness of fynbos-typical birds in the artificial fragments that are surrounded by human land uses and is tested in Chapter 4.

2.3.4 Introduced species

As I have mentioned, fragmented communities often respond directly to the constraints of the fragmented habitat and surrounding matrix. The surrounding matrix however, often introduces new pressures to fragment communities such as invasive species (Saunders et al., 1991; Hobbs & Yates, 2003; Buckley et al., 2006; Hulme, 2006; Lindenmayer & Fischer, 2006), novel disturbances (Rouget et al., 2006; Kongor, 2009) and environmental fluxes (Saunders et al., 1991; Brotons et al., 2003), to which fragment communities also respond. Matrix specific species, such as crop plants or cosmopolitan weeds in the case of an agricultural matrix, can potentially colonise a habitat fragment and interact with local species (Saunders et al., 1991; Gascon et al., 1999; Hulme, 2006). Generalist faunal species that are attracted by the altered matrix habitat can also enter habitat fragments and influence fragment communities (Saunders et al., 1991). The specific invasibility of a fragment varies between fragment communities, and is generally associated with a disturbance event (Saunders et al., 1991). The manner by which invasive species, plant species in particular, enter a fragment can vary (Richardson et al., 2000). Species that are dispersed over some distance by a vector, such as a frugivorous bird, livestock or the wind, may colonise a fragment in a random pattern or according to the pattern of movement of the dispersal vector. For example, ornithochorous tree species may establish around bird perch sites within a fragment (Phillips, 1927, and see Chapter 3, Section 4 and Chapter 4, Section 4.4). Other species that do not rely on a specific dispersal vector may only successfully colonise the perimeter of a fragment, as far in as edge effects and disturbances penetrate (Cale & Hobbs, 1991; Panetta & Hopkins, 1991; Saunders et al., 1991; Kupfer et al., 2006).

2.3.5 Novel disturbances

Matrix heterogeneity has at times been found to increase local species persistence and dispersal in fragment systems (Gustafson & Gardner, 1996; Vandermeer & Carvajal, 2001), however it is also possible that more heterogeneous or diverse matrix habitats are associated with a greater variety of matrix-typical invasive species that can colonise habitat fragments and influence local species. This is tested using matrix-typical vegetation data in Chapter 4, (Section 4.4). Saunders et al. (1991) identified various changes that occur to the microclimate of habitat fragments. Specifically water, wind and radiation fluxes were recognised. These fluxes are also termed edge effects (Kapos, 1989; Fagan et al., 1999). The extent to which an edge effect can influence fragment communities depends on the distance that the effect can penetrate into a fragment from its boundary (Fagan et al., 1999) and

on the size and shape of the specific habitat fragment. A roughly circular fragment may have more unaffected area in its centre or core area where environmental fluxes cannot reach than a more linear fragment of similar total area (Fagan et al., 1999).

Habitat fragmentation also affects disturbance regimes to which fragmented communities respond (Baker, 1994; Mack & D'Antonio, 1998; Brooks et al., 2004; Kupfer et al., 2006). Natural disturbance regimes such as periodic fire in grassland (McNaughton, 1983; Hobbs & Huenneke, 1992; Bond et al., 2005) and in certain mediterranean-type ecosystems (Kruger & Bigalke, 1984; Keeley, 1986; Bond et al., 1988; van Wilgen et al., 1992; Goldblatt & Manning, 2000) are important aspects of ecosystems and often contribute to maintaining diversity (Sousa, 1984). Using the example of fire; when fire-prone habitats are fragmented by fire-suppressive land-uses, the resulting fragment patches are isolated from the spread of fire (Turner et al., 1989; Andrén, 1994; Hargrove et al., 2000; Kupfer et al., 2006). Bond et al. (1988) established that fire isolation was the cause of historic species extinctions in the fynbos vegetation of the natural islands which were naturally fragmented by fire-suppressive indigenous forest (Midgley & Bond, 1990; Mucina & Geldenhuys, 2006). The isolation of disturbance regimes in fragmented ecosystems is thus governed by similar principles to those involved with the isolation of biological communities.

Parallels between the effects of fragmentation on communities and disturbance regimes are also seen with respect to reduced fragment area. Using the example of fire again; smaller fragments will have fewer sources of ignition than larger fragments and, in the case of ignition by lightning strike or by wind-driven cinders, smaller fragments will provide a smaller target and thus are less likely to receive their required fire regime (Pickett & Thompson, 1978; Bond et al., 1988; Geldenhuys, 1994). For this reason, the assumed fire-area relationship in the natural fynbos islands is tested using historic fire data in Chapter 3 of this study. This is analogous to the target effect derived in island biogeography theory (Whitehead & Jones, 1969; Lomolino, 1990), as mentioned previously. Inversely, a matrix habitat may serve as a disturbance "super-conduit" (Franklin & Forman, 1987; Kupfer et al., 2006) whereby natural disturbances are transmitted across the matrix to habitat fragments at a frequency or intensity that is detrimental to fragment communities. Either way, the specific nature of the matrix that surrounds a habitat fragment can alter the natural disturbance regime within the fragment.

Aside from the manner in which the matrix can alter the natural disturbance regime in habitat fragments, novel disturbances that originate in the matrix can affect fragment communities (Kupfer et al., 2006). Hulme (2006) highlights how the grazing of fragment vegetation by livestock from bordering farmlands can function as a novel disturbance through which invasive alien plants can enter and establish in a fragment. This grazing can facilitate the introduction of invasive plant species and the increase of invasive plant abundance within a fragment (Mack, 1989; McClaran & Anable, 1992). Additional to these indirect effects, livestock grazing can pose a more direct threat to local vegetation when more palatable local species are selectively grazed and less palatable invasive species are overlooked (McClaran & Anable, 1992; Hulme, 2006; Todd, 2006). Kemper et al. (1999) found that small fragments of renosterveld shrubland in South Africa's Cape Floristic Region are largely disturbed through trampling and grazing by livestock and by crop spraying, and that these fragments receive fire of human origin more frequently than non-fragmented areas. The application of island biogeography theory to fragmentation science has been criticised for ignoring the influence of matrix habitat. It is apparent however from the literature that the matrix primarily alters the effective habitat area and level of isolation of a fragment for local species or for the disturbance regimes on which they depend. Island biogeography theory, which describes the effects of area and isolation, can thus present a useful framework through which to study the effects of habitat fragmentation on local communities, provided that it is used in conjunction with an understanding of the fragmented system in question.

This understanding should cover the nature and motility of local biological communities, the nature of the surrounding matrix and the nature of any natural disturbance regime that is specific to the ecosystem being studied. In this study the natural islands are used to assess the effect of fragment area and isolation on fragmented communities, through the island biogeography framework (see Chapters 3 and 4), and the artificial fragments are used to assess the effect of the modified surrounding matrix on these communities (see Chapter 4). The effect of the matrix may be inferred from the difference between the biological communities of the two habitat configurations.

2.3.6 Ecological relaxation

Another aspect of habitat fragmentation that requires consideration when studying or managing fragment communities is the amount of time elapsed since a fragment became isolated by some landscape modification (Saunders et al., 1991; Ewers & Didham, 2006). Unlike the other main aspects of fragmentation – fragment area, degree of isolation and the nature of the surrounding matrix – time since isolation is not a physical constraint but can rather be seen as the amount of time given for a community to respond to the physical constraints of their habitat fragment. Communities may only show a response to fragmentation effects long after the fragmentation event has occurred (Tilman et al., 1994; Helm et al., 2006; Krauss et al., 2010). The equilibrium theory of island biogeography and its subsequent developments recognised that the dynamic equilibrium state of island habitats is unique to every island; the rates of immigration and extinction that determine this state are governed by the physical characteristics of the island and the nature of the organisms that inhabit the island (Preston, 1962; MacArthur & Wilson, 1963, 1967; Whitehead & Jones, 1969; Simberloff, 1974; Brown & Kodric-Brown, 1977). From this it can be implied that a change in the physical characteristics of an island will cause the rates of immigration and extinction and the final equilibrium state to shift accordingly. Wilson and Simberloff (1968; 1969, 1970) ran a controlled experiment that simulated island formation in order to analyse the role of immigration and extinction in insular habitats. They found that equilibrium was eventually reached but only after a period of time during which the stable rates of immigration and extinction became established. Diamond (1972) conducted a natural experiment in which he examined land-bridge islands with a known time-since isolation (Malanson, 2008). In their current isolated state, these islands cannot support their former equilibrium level of species richness, however not all of the islands were found to have reached their new, predicted equilibrium state. This process of delayed extinction is known of as ecological relaxation (Diamond, 1972; Gonzalez, 2000; MacHunter et al., 2006; Malanson, 2008). Diamond's work complimented that of MacArthur (1972) which examined ecological relaxation as a direct development of the equilibrium theory of island biogeography (MacArthur & Wilson, 1963, 1967) as established by himself and Wilson a few years before.

2.3.7 Extinction debt

Parallels can be drawn between land-bridge islands and habitat fragments with respect to time since isolation in that both cases involve a formerly connected habitat supporting a full complement of local species prior to an isolation event (Pickett & Thompson, 1978; Faaborg, 1979). In fragmentation science, the difference between this former equilibrium level and the new, post-fragmentation level is termed the 'extinction debt' of a fragment community (Tilman et al., 1994; Malanson, 2008; Kuussaari et al., 2009; Hylander & Ehrlén, 2013). This term implies that the new equilibrium level is not reached instantly but rather through a series of time-delayed extinctions. From a conservation point of view, this debt can either be paid through local species extinctions or through management interventions, such as the provision of certain resources or the conservation of connecting corridors between fragments (Tilman et al., 1994; Brooks et al., 1999; Kuussaari et al., 2009; Hylander &

Ehrlén, 2013). In the same way that extinction debt can be observed and quantified, so can the process of immigration credit which follows an upward shift of a fragment's equilibrium state (Hanski, 2000; Jackson & Sax, 2009; Lira et al., 2012). This can occur through processes such as the expansion of a habitat fragment's area (Perz & Skole, 2003; Rudel et al., 2005; Baptista & Rudel, 2006) or the facilitation of better connectivity between fragments (Wilson & Willis, 1975; Beier & Noss, 1998), leading to fragment conditions supportive of a larger biological community.

The principle of extinction debt in fragmented communities, as first explained by Tilman et al. (1994), predicts that the order of species extinctions and the rate at which the debt is paid (Vellend et al., 2006) is determined by the mobility and the competitive ability of local species. Specifically, highly motile species, such as fynbos-typical birds, will persist for longer than sedentary species, provided that the system of habitat fragments has sufficient metapopulation potential and species can migrate between fragments. For this reason I examine the response of motile fynbos-typical birds to recent fragmentation in Chapter 4, and compare this response to that of sedentary fynbos plants, as investigated in Chapter 3. Tilman et al. (1994) showed that when species that are strong competitors are also weak dispersers, they are more at risk to fragmentation-related extinction and are thus generally 'paid' first. Extinction debt may linger far longer in species that are strong dispersers.

Recent literature on extinction debt has considered the role of species traits other than motility and competitive ability in determining the order of extinction in fragmented communities. Individual species such as certain plants are characterised by long generation times (Kuussaari et al., 2009; Garcia et al., 2011), resistant life-cycle stages (Eriksson, 1996; Mergeay et al., 2007; Hylander & Ehrlén, 2013) and those species that persist just below their extinction threshold (Hanski & Ovaskainen, 2002; Kuussaari et al., 2009) are generally prone to time-delayed extinctions. Extinction debt may persist for longer in metapopulation situations where species turnover rates are characteristically slow (Hylander & Ehrlén, 2013). Small fragment communities may lose species in a collective manner through stochastic environmental events which are not associated with their fragmentation (Lande, 1993; Dennis, 2002). Therefore these extinctions will only occur sometime after fragmentation (Hylander & Ehrlén, 2013). South Outeniqua Sandstone Fynbos vegetation is characterised by post-fire regeneration cycles which are often decades long (Southey, 2009; Kraaij et al., 2012a, 2013a). Lightning strike is the natural source of ignition (Kraaij et al., 2012b). Plants that have fire-cued germination rely on a specific fire-return interval (Kruger, 1983; le Maitre & Midgley, 1992, and see Chapter 3, Section 1). When a fynbos island goes without fire for too long, certain species will go locally extinct (Kraaij et al., 2013a, 2013b). Because lightning strike in the small islands is relatively stochastic, some fire-return intervals may be exceptionally long, resulting in episodic extinctions occurring sometime after an initial fragmentation event. Because the natural islands have been isolated since the early Holocene (Midgley & Bond, 1990) it is assumed that their vegetation communities have undergone ecological relaxation and represent a stable equilibrium or quasi equilibrium level. I test this assumption in Chapter 3 (Section 3.2) and go on to compare the vegetation species richness in the artificial fragments to that in the natural islands in order to investigate the presence of extinction debt.

The scarcity of reliable long-term community data from habitat fragments has limited investigations to studies that identify the presence of extinction debt; few studies have been able to empirically quantify the phenomenon (Kuussaari et al., 2009; Lira et al., 2012). The various approaches that have been used to study extinction debt in fragmented communities (Kuussaari et al., 2009; Lira et al., 2012) have had to draw inferences from current observations in various habitat configurations – fragmented and natural (Berglund & Jonsson, 2005; Helm et al., 2006; Vellend et al., 2006; Kuussaari et al., 2009; Lira et al., 2012). The empirical investigation of extinction debt cannot yet be considered

a precision science, however the broad trends of time-delayed extinction that can be observed in fragmented communities play an important role in conservation science (Malanson, 2008; Jackson & Sax, 2009; Kuussaari et al., 2009; Wearn et al., 2012; Hylander & Ehrlén, 2013). These trends can provide information about species or functional group vulnerability to fragmentation or to the constraints of sub-optimal reserves (Eriksson, 1996; Korner & Jeltsch, 2008; Malanson, 2008; Hylander & Ehrlén, 2013). In this regard they also have application in the design of effective reserve networks (Pickett & Thompson, 1978). The unique landscape mosaic that is used in this study provides an opportunity to investigate extinction debt by using the natural islands as a model (Chapter 3). As mentioned previously, an extinction debt can be 'paid' through local extinctions or through management intervention. Therefore the detection of extinction debt in fragmented communities affords management the chance to prevent future extinctions that may result from past fragmentation events (Kuussaari et al., 2009; Wearn et al., 2012; Hylander & Ehrlén, 2013).

2.4 THE ECOLOGY AND DYNAMICS OF FYNBOS

Fynbos is an extremely diverse mediterranean-type ecosystem that occurs in the Cape Floristic Region of South Africa (Goldblatt, 1978; White, 1983; Takhtajan, 1986; Rebelo et al., 2006). The high levels of vegetation diversity are associated with a particular fire regime which varies in terms of fire frequency, intensity and seasonality (Bond & van Wilgen, 1996; Thuiller et al., 2007). Bond et al. (1988) found a significant island species-area relationship in isolated South Outeniqua Sandstone Fynbos (Rebelo et al., 2006) vegetation communities which occur as naturally fragmented habitat 'islands', separated from the more extensive 'mainland' areas by indigenous forest (see Chapters 1 and 3). They attributed this relationship to the unique fire return interval that each island receives through interaction between lightning strike frequency and the specific geology of each island: small islands are a smaller target and so receive fewer strikes than large islands. These large islands get burned more frequently (See Chapter 3, Figure 3.1) and have a fire return interval that better resembles the mainland areas (Pickett & Thompson, 1978). The larger islands therefore accommodate similar plant species richness and composition to the mainland areas. Thuiller et al. (2007) found that the coexistence of fynbos species that is necessary within such a highly diverse community relies on some stochasticity of this fire regime. Temporal stochasticity through variation in the three abovementioned components of the fire regime drives niche turnover and thus allows for the temporary proliferation of certain species within a community. If this stochasticity is reduced because of reduced variability in one or more of the regime components, the post-fire ecosystem will consistently be dominated by the same species, leading to reduced coexistence and increased likelihood of local extinctions. The consistently over-extended fire-return intervals that have been proposed in the natural islands may have led to communities dominated by long-lived, slow maturing species.

2.5 PRACTICAL APPLICATION

Through this review one can trace the development of a branch of landscape ecology from primary literature concerned with islands and the equilibrium theory of island biogeography (e.g. Preston, 1962; MacArthur & Wilson, 1963, 1967; Diamond, 1969; Simberloff, 1974) through to studies of the more contemporary issues of habitat fragmentation and extinction debt (e.g. Saunders et al., 1991; Tilman et al., 1994; Hanski, 2000; Laurance, 2008; Malanson, 2008; Kuussaari et al., 2009; Hylander & Ehrlén, 2013). Much debate has transpired concerning the response of biodiversity to the natural and human-induced isolation of habitat areas and also concerning the use of equilibrium theory in the study of the biological communities that occupy these habitats. From these developments it can be seen that not all communities respond to the various pressures of fragmentation in a similar way, and

that not all of the pressures associated with fragmentation will have the same effect on a biological community. Thus no one general theory can be used to assess the manner in which biodiversity will respond to the future of increased habitat fragmentation that we are faced with. Instead, the various theories that have attempted to do this in the past should be used as frameworks, together with an understanding of the unique dynamics of each fragment community, through which to investigate individual fragment community responses. I have consulted the wealth of literature and used many examples of other fragmentation studies in the design of this study, which will attempt to investigate the response of certain fragmented communities and to complement the fields of island biogeography and fragmentation science.

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CHAPTER 3 – COMMUNITY STABILITY IN THE FYNBOS ISLANDS: THE ROLE OF ISLANDS IN UNDERSTANDING EXTINCTION DEBT

3.1 INTRODUCTION

Reserve selection and the prioritisation of certain areas for conservation have long been debated in the scientific literature (Diamond, 1975; May, 1975; Wilson & Willis, 1975; Simberloff & Abele, 1976; Ovaskainen, 2002). Stemming from initial conversations, such as the SLOSS (single large or several small) debate (see Chapter 2, Section 2.3), conservation planners now have an overwhelming choice of tools available to them (Pressey et al., 1993; Kitzes & Merenlender, 2013). These tools are designed either to maximise the persistence of certain species of conservation importance or to maximise the persistence of biodiversity through the selection of priority areas within a landscape (Williams et al., 2004). When reserve networks are chosen according to the latter priority, compromises are bound to occur due to the complexity of biological communities and also due to the limited resources that are typically available to conservation planners (Leader-Williams & Albon, 1988; Pressey et al., 1993; James et al., 1999; Balmford & Whitten, 2003). Certain species will be better off in many small reserves, provided that the reserves are sufficiently aggregated to maintain dispersal (Simberloff & Abele, 1976), while others may require one or more large reserve, particularly when species are non-motile or when dispersal ability is limited (Tilman et al., 1994). Of course, the optimal solution to the SLOSS debate would be to select many large reserves that are effectively linked and have the smallest possible perimeter (Wilson & Willis, 1975; Williams et al., 2004), but in reality this is seldom an option (Diamond, 1975; Saunders et al., 1991; Ewers & Didham, 2006). In fact, networks of many small reserves are more common and each reserve is often selected to preserve a certain component of a region's biodiversity. Each small reserve then has a high degree of irreplaceability and has to be managed and maintained correctly given that it is integral to the success of the entire reserve network.

Small reserves also require more complex management than large reserves because they increasingly resemble islands surrounded by a human-modified matrix. The communities inhabiting these 'artificial islands' will be subject to area- and isolation-related demographics as are oceanic and habitat islands (MacArthur & Wilson, 1963, 1967; Diamond, 1975). Island biogeography theory states that island communities will reach a state of equilibrium when the rates of immigration and extinction are equal, and that this state will be unique to an island's area and degree of isolation (MacArthur & Wilson, 1963, 1967, and see Chapter 2, Section 2.2). The island biogeography theory has been largely modified and amended since its origin to address the large assumptions that it makes (eg. Brown & Kodric-Brown, 1977), however the original theory, the amendments and the broad application of the theory in conservation and ecological science has been biased towards faunal communities (e.g. MacArthur & Wilson, 1963, 1967; Brown, 1971; Diamond, 1972, 1975). In reserve selection, the requirements of the vegetation community are also often overlooked and small reserves are selected for the irreplaceability of their faunal inhabitants (Pressey et al., 1993; Panzer & Schwartz, 1998).

A contemporary application of island biogeography theory is in habitat fragmentation theory (Haila, 2002, and see Chapter 2, Section 2.3). Following the isolation of small fragment patches through habitat loss there is often a lag period during which the rates of immigration and extinction shift until a new state of quasi equilibrium is reached (Diamond, 1972; Tilman et al., 1994, and see Chapter 2, Sections 3.6 and 3.7). The resulting community will be less diverse than prior to its fragmentation and the difference between the two equilibrium states is termed the "extinction debt" owing to the fact that

it is to be paid – through localised species extinctions or through management prescription – in the future (Tilman et al., 1994; Kuussaari et al., 2009; Hylander & Ehrlén, 2013). The time taken for this debt to be paid, or the ecological relaxation time, is governed by the biology of the species threatened by extinction (Vellend et al., 2006) and in this case by the biogeographic nature of the reserve network. Motile species that are capable of forming metapopulations will increase the relaxation time, provided that the reserve network permits their movement (Tilman et al., 1994). The response of faunal species to small reserve patches may be immediately obvious, particularly for species that are incapable of migrating between reserve patches.

Some plant species have characteristically long lifespans (Ewers & Didham, 2006; Vellend et al., 2006; Garcia et al., 2011; Hylander & Ehrlén, 2013) and, if unable to disperse their seeds beyond the reserve boundary or if they are reliant on some other vector which may be missing from the system to disperse their seeds, they may be completely incapable of utilising the metapopulation potential of small-reserve networks. This leaves them confined to individual reserves which may be too small to support seedling recruitment (Diamond, 1975; Saunders et al., 1991). Vegetation communities often develop through successional stages or through post-disturbance regeneration cycles which, if undisturbed by fragmentation, may take many years to run their course (Horn, 1975). It is also likely that isolated communities such as these will become suspended in one state, unable to make the transition to the next state in the absence of the required propagules from neighbouring vegetation. Plant species in small reserves are also subject to prominent edge effects which may not be detrimental to established individuals, but which can prevent the germination and development of propagules (Saunders et al., 1991; Meiners et al., 2000; Tomimatsu & Ohara, 2004). The formation of a small reserve may therefore not result in an immediate response from the vegetation community (Pickett & Thompson, 1978; Ewers & Didham, 2006; Vellend et al., 2006) and plants can represent an insidious component of the extinction debt that small reserve communities often hold (Saunders et al., 1991; Kuussaari et al., 2009; Hylander & Ehrlén, 2013). If this component is overlooked, a small reserve may be rendered less effective for the conservation of the vegetation community or even of the faunal species which rely on the vegetation community as a resource.

The quantification of extinction debt along with an understanding of which species are most threatened by it is very important for both the selection of reserve size and for the management of small reserves (Pickett & Thompson, 1978). This knowledge can be obtained from communities existing in island-like refugia or natural fragments. Examples include fynbos islands in South Africa's Southern Cape forests (Midgley & Bond, 1990, and see Chapter 1, Section 1) edaphically isolated habitat islands in northern Patagonia (Kim et al., 1998) and quartz patches found in the Succulent Karoo, South Africa (Ellis & Weis, 2006), forest patches in the grasslands of the Nyika Plateau in Malawi (Dowsett-Lemaire, 1985; Willis et al., 2001) and the land-bridge islands in New Guinea (Diamond, 1972).

I focus on the fynbos islands in the Southern Cape because I had access to historic data from these patches, because the area is characterised by a landscape mosaic particularly suited to the study and because the natural islands have been isolated for long enough for any potential community changes to have occurred. Because the indigenous vegetation – South Outeniqua Sandstone Fynbos (Rebelo et al., 2006) – is fire-adapted and develops through cycles of post-fire regeneration (see Chapter 1, Section1 and Chapter 2, Section 4), community response to fragmentation may only become apparent after successive fire-return intervals (Eriksson, 1996; Mergeay et al., 2007; Hylander & Ehrlén, 2013). If the fire return interval is overextended, certain fire adapted species and their seeds may senesce (Bond, 1980; van Wilgen, 1982). Therefore the extinction of fynbos-vegetation species from such a community is closely related to the fire return interval in that community. This vegetation-type

naturally occurs as large tracts termed 'mainlands' and smaller fynbos islands which were isolated by climate-driven forest expansion during the early Holocene (Midgley & Bond, 1990). These natural islands are effectively isolated from the spread of wildfire through the surrounding Southern-Afrotemperate Forest[1] (Bond et al., 1988; van Wilgen et al., 1990; Mucina & Geldenhuys, 2006; Rebelo et al., 2006) and rely on lightning strike as a source of ignition. However, lightning strike is not constant on all sized islands but is governed by a target effect (Bond et al., 1988; Wardle et al., 2003) similar to that which typically influences the rate of immigration in conventional island biogeography theory (Whitehead & Jones, 1969). Small islands are assumed to present smaller targets than large islands and receive disturbances such as lightning strike less frequently (Pickett & Thompson, 1978; Bond et al., 1988, and see Chapter 2, Section 3.5). Therefore they will have an over-extended fire return interval and, as shown by Bond et al. (1988), their vegetation communities have responded through the local extinction of certain species – low shrubs and fire-dependant species in particular. Thuiller et al. (2007) showed that the consistent removal of stochasticity from the local fire regime in a fynbos community will have implications for species coexistence and can lead to species extinctions. The stochasticity of the fire regime in the natural fynbos islands is reduced by the consistently over-extended fire-return interval.

More recently a number of artificial fragments have resulted from the destruction of mainland habitat through development, cultivation and plantation forestry (Rebelo et al., 2006, and see Chapter 1, Section 1). With over 28% habitat loss, South Outeniqua Sandstone Fynbos is classified as being vulnerable (Rebelo et al., 2006) giving this mosaic high conservation importance. It should be possible to replicate this study in other 'land island' type communities such as those mentioned previously and also in other mediterranean-type ecosystems characterised by fire-isolated communities.

By observing the response of vegetation communities to fragmentation in isolated patches that have reached a new equilibrium state (model communities) and also in more recently isolated fragment patches that are still undergoing ecological relaxation, or in a mainland site, I quantify the magnitude of the extinction debt for a particular sized fragment (Pickett & Thompson, 1978; Kuussaari et al., 2009, and see Chapter 2, Section 3.7). By examining the type of species that have already gone extinct in the model communities and comparing this to the species composition of the mainland community I identify which species groups are most at risk to extinction following habitat fragmentation. I believe that this type of information will help conservation planners to select reserve patches that will adequately maintain the vegetation community and hence also those faunal species reliant on it (Panzer & Schwartz, 1998; Sætersdal et al., 2003). Also, having information regarding the vulnerability of individual species groups to small reserve sizes will equip reserve managers to make effective prescriptions in cases where the opportunity for large reserves is not available, or where small reserves have already been proclaimed.

My aims include: an examination of the effect of fynbos habitat size on fire-return interval; an investigation into the relative stability of the natural island plant communities over a 24 year period using simple census techniques; an assessment of the plant community response to the artificial fragmentation of mainland habitat, focussing on the response to patch area. By comparing natural island and artificial fragment communities, I aim to quantify extinction debt that may exist and

[1] Wildfire has been known to spread in a 'skipping' fashion as cinders blowing from the tops of ridges that lie in the path of hot winds known locally as 'bergwinds' (Geldenhuys, 1994). Although fire seldom spreads through the indigenous forest, it can reach the isolated patches via this process. It is however more likely for a cinder to reach a large fynbos patch than a small one

determine which species are most at risk. Through this I assess the value of using simple inventory data in the detection of extinction debt in small reserve communities and thus in the process of reserve selection and reserve management.

3.2 MATERIALS AND METHODS

3.2.1 Study area

A detailed description and map of the study area can be seen in Chapter 1, (Section 1) and in Rebelo et al. (2006).

3.2.2 Site selection

A total of 68 units of South Outeniqua Sandstone Fynbos were sampled, of which 36 were mainland plots (large, continuous tracts of habitat), 16 were natural islands (embedded in a forest matrix) and 16 were artificial fragments (embedded in a range of land-use types). The mainland was sampled as three series of 12 fully nested plots (see Dengler, 2009) with individual plots increasing in size (1 ha; 2 ha; 4 ha; 6 ha; 10 ha; 15 ha; 20 ha; 25 ha; 35 ha; 50 ha; 75 ha; 110 ha). The mainland series were situated on two large areas (>300 ha)[2] of fynbos. Currently there is relatively little old-growth fynbos in the study area (Kraaij et al., 2012), particularly in the mainland areas. These two sites were chosen to include some young growth and some old growth vegetation so as to produce a mean post-fire vegetation age that is more representative of the mainland areas in general. This was done in order to minimise the effect of differently aged vegetation in certain plot sizes categories. I attempted to arrange the plots so that a mean vegetation age was achieved throughout the resulting average mainland series.

Natural islands were chosen primarily to correspond with those sampled in 1988. Following this, more natural islands and the artificial fragments were chosen to represent a range of different areas, degrees of isolation and according to the quality of documented management history (Kraaij T, unpublished data). Artificial fragments were also chosen to represent a range of different matrix types. Most of the fragments were isolated from the mainland during the past one and a half centuries through afforestation (Kraaij & van Wilgen, 2011). Although exact dates could not be found, all 16 fragments have been isolated for over a century (Kraaij & van Wilgen, 2011). In some cases this plantation forestry matrix has been replaced by agriculture, or by dense, unmanaged stands of invasive alien plants.

The fragments are often surrounded by more than one matrix type and three dominant types are recognised. These include farmland, timber plantations and Southern-Afrotemperate Forest (Mucina & Geldenhuys, 2006). Dense stands of invasive alien vegetation border some of the artificial fragments. In this study these areas have been grouped together with the plantation matrix type, since both contain similar species and present similarly homogenous vegetation. Two other matrix types include dams and differently aged fynbos. Together these matrix types contributed so little (3%) to the

[2] 300 ha was identified as the minimum critical fynbos island size, beyond which no island effects were noticed and a mean value of 590 ha was then chosen as the critical value (Bond et al., 1988). Short of jeopardising the integrity of my results by selecting large mainland sites with high altitudinal variation, I selected sites that lay between the mean and the minimum area value but which had more altitudinal consistency. Both of the chosen sites are naturally part of the mainland although recent agricultural and urban expansion has limited their connectivity.

average fragment boundary that they were not included in the study[3]. There are two cases in which an artificial fragment is bisected by a large road that has functioned in the past as a fire break. A unique fire history exists for each separate section of the fragment. These fragments were treated as two independent study sites.

Most of the study sites are found within the Garden Route National Park, while some of the artificial fragments are situated on private land. All sites lie within: 22°51'57.02"E- 23°14'24.09"E/ 33°53'2.58"S -34° 4'41.92"S. The physical attributes of the individual sites are given in Appendixes 3.A and B.

3.2.3 Methods

Data collection was based on the methods used in Bond et al. (1988). Community data were captured by walking wandering transects through a designated fynbos patch and counting species until the rate of new species discovery plateaued at less than two new species per hour. At this point it was assumed that all species existing in the patch had been discovered. Species were identified and noted in the field whenever possible and vegetation samples or photographs were collected for unknown species. Reference books (Courtenay-Latimer et al., 1967; Moriarty, 1982; Coates Palgrave, 1983; van Wyk & van Wyk, 1997; van Oudtshoorn, 1999; Goldblatt & Manning, 2000; Manning, 2007) were used in conjunction with local botanical experts and citizen scientist groups to identify species and to classify them according to functional type. This approach is somewhat qualitative in nature. It is however less time consuming than other, more elaborate methods (Bibby et al., 1992) and a greater coverage of study sites could be achieved. Additionally, the vast documentation of fynbos-specialist species allowed for the calculation of functional trait abundances from these species counts in the different patch configurations.

Mainland sites were sampled in a similar manner. Siting was pre-determined using Google Earth Pro on 2011 images in an elevation range of between 500 m and 1500 m and plot boundaries were maintained during data collection using a hand-held GPS device with pre-loaded waypoints. As was done in 1988, the mainland was sampled as fully nested plots (see previous section) in an accumulative manner. For example, if a certain species which had already been identified in an earlier plot was found again in a subsequent plot, it was not counted again. Thus the species richness in the second plot equalled the sum of the species counted in the first and second plots, and so on. Regressions that resulted from this approach were tested in 1988 against those drawn from randomly located plots and the difference was found to be insignificant (Bond et al., 1988). This approach limits the investigation of the mainland data to regression analysis and hypotheses cannot be tested between the different sized plots. However it is far more time efficient than ‘single-value’ methods in which individual, non-nested plots are used. This efficiency allowed a larger sample size to be included in the study.

The physical attributes of each site were calculated using Google Earth Pro on 2011 images in an elevation range of between 500 m and 1500 m and are shown in Appendixes 3A and 3B. Historic species data were obtained from W.J. Bond and historic fire data were obtained from T. Kraaij, courtesy of South African National Parks. Fire data extend back over a century; however their accuracy beyond twenty years is not certain in that they are based on the historic accounts of various

[3] Differently aged fynbos is not strictly speaking a matrix type since it only occurred within the boundaries of fynbos fragments. One should not be led to believe that these fragments are in fact connected to a fynbos mainland through a tract of differently aged fynbos.

witnesses and observers. These data do however provide a broad overview of pattern of recurrent fire on differently sized fynbos habitats.

3.2.4 Statistical analysis

Historic fire data were used to group fynbos sites according to the number of fires received in recorded history, ranging from none to four fires. The frequencies of these four groups were then analysed through ordinary least squares regression in Microsoft Excel 2010: Analysis ToolPak.

Inventories that included species attributes and functional traits were compiled. Ordinary least squares regressions to assess the response of species to patch area were run using only fynbos-typical vegetation (see Appendix 3.C) species data that were log-transformed (see Cook et al., 2002). Regressions were calculated for the subset of the natural island sites that corresponded with those included in the 1988 study. One natural island that was used in 1988, "NI041", could not be reached during the 2012 study and therefore it was substituted for "NI050". "NI050" is similar to "NI041" in terms of area, location, altitude and fire history (Kraaij, unpublished data). An average was obtained from the three mainland series for each plot size, which was then used in the mainland regression. This corresponded with the methods used in 1988. The regression that was run for the artificial fragments included all 16 of the fragments patches.

Regression curves were tested against each other using a simple regression comparison in Microsoft Excel 2010. Regressions were tested for change in either the mainland or the natural islands over 24 years and for differences between the three fynbos configuration types.

Modified Chi-square tests were used to investigate functional trait and habitat-specialist distribution between the 1988 and the 2012 data sets, and between the present day mainland, natural islands and artificial fragments. These were similar to those used by Bond et al. (1988). The 1988 data were used to calculate expected values. This required the scaling of the frequencies of each variable to the species total of the 2012 data, which were used as the observed values (see Bond et al. 1988). The null hypothesis was that the frequencies in each variable category do not differ between the observed and the expected. Only fynbos-typical species data were used to analyse functional trait distribution while complete inventory data were used to analyse habitat-specialist distribution.

In order to illustrate where and how the isolated configurations have responded to fragmentation, the total species inventory was categorised into various habitat-typical species for each of the three fynbos configurations (mainland, natural islands and artificial fragments). The two isolated configurations were then compared against each other in terms of relic species, species added and species lost relative to the mainland. These totals are presented descriptively.

3.3 RESULTS

3.3.1. Fire frequency and area

The number of recorded fires in habitat areas of South Outeniqua Sandstone Fynbos (including all three habitat configurations) within the Garden Route National Park has a significant positive relationship ($p < 0.001$; $R^2 = 0.204$; $SE < 0.001$) with the size of the habitat (Figure 3.1). Only fynbos areas that are over 100 hectares have been recorded to have burned up to three times, and no fynbos areas that are over 300 hectares have remained fire-free in recorded history.

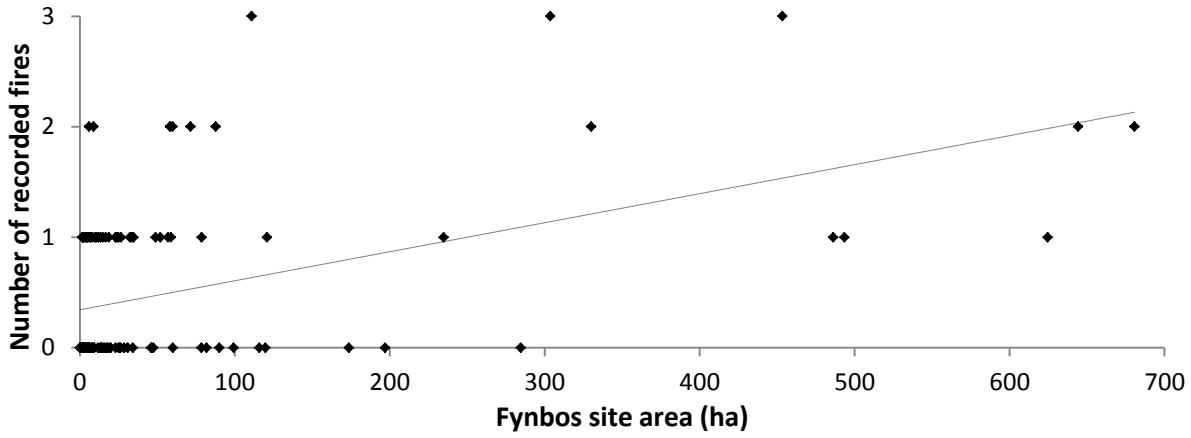

Figure 3.1 – Relationship between the number of recorded fires since 1900 and the area of South Outeniqua Sandstone Fynbos sites within the Garden Route National Park. Data are courtesy of South African National Parks.

3.3.2 Natural islands over twenty-four years

The plant species richness of the mainland plots is significantly related to sample area (Table 3.1, Figure 3.2.A). There is also a significant island species-area relationship found in the natural fynbos islands (Table 3.1, Figure 3.2.A). Included are the regression results from Bond et al. (1988) which display the significant species-area relationship observed in both the mainland plots and in the natural fynbos islands (Table 3.1, Figure 3.2.A).

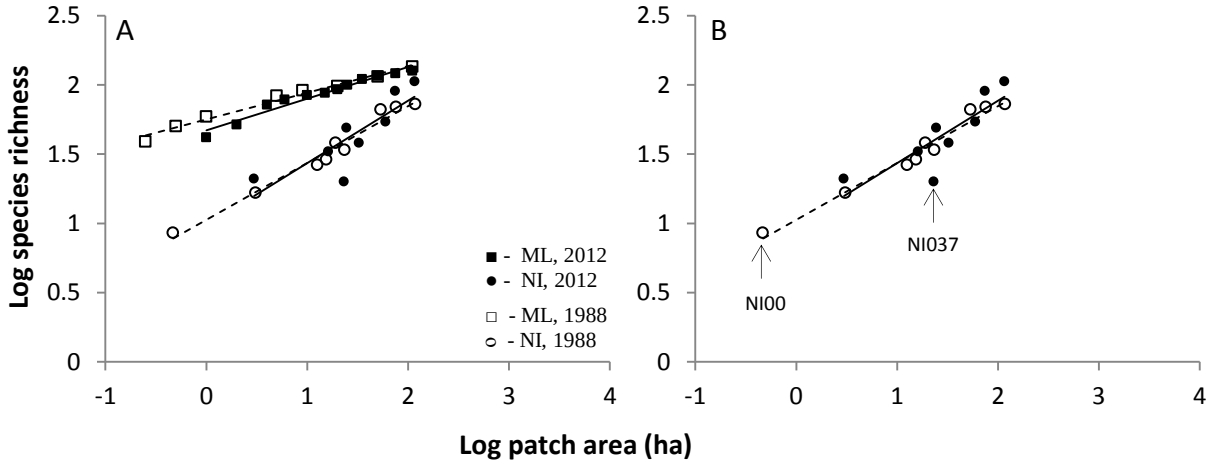

Figure 3.2 – The linear regression relationships between the number of fynbos species (logged) recorded and the logged area of the fynbos patch. ML= mainland and NI = natural islands. Solid trend lines show relationships in the recent data (2012) and dashed trend lines show relationships in the historic data (1988). (A) Illustrates the regression lines of the mainland plots and the fynbos islands and compares them to that found in 1988. (B) Illustrates the regression lines for the natural islands with emphasis on the outliers.

The regression slopes for the mainland and for the natural fynbos islands have not changed significantly since 1988 (Table 3.2, Figure 3.2.A). This is despite the influence of a natural island outlier, namely "NI037" observed in the 2012 island species-area curve (Figure 3.2.B). The absence of "NI00" in 2012 is also noted (Figure 3.2.B). "NI037" exhibits lower species richness than the general trend for the natural islands. This island's vegetation is dominated by the fern *Gleichenia polypodioides*, which appears, wherever it dominates, to form dense homogenous stands in which only a few forest and even fewer fynbos species can persist (See Figure 3.3). The smallest natural

island that was sampled in 1988, "NI00", was indistinguishable from the surrounding natural forest in 2012 and so it was not sampled.

Table 3.1 – The relationships between fynbos vegetation species richness and area for mainland (ML) plots and for natural islands (NI), tested through linear regression. (1) Shows relationships found in the historic data (Bond et al. 1988) and (2) shows those found in the recent data (2012). (3a) presents the species-area regression results from data collected in the artificial fragments.

	Data	R	1 SE	*t*-value	*P*-value	R^2
1a)	$ML_{'88}$	0.19	0.011	17.03	< 0.0001	0.98
b)	$NI_{'88}$	0.41	0.026	15.66	< 0.0001	0.97
2a)	$ML_{'12}$	0.23	0.015	15.05	< 0.0001	0.96
b)	$NI_{'12}$	0.45	0.120	3.71	$\ll 0.010$	0.70
3a)	$AF_{'12}$	0.10	0.052	1.93	> 0.050	0.21

ML= mainland, NI= natural islands, AF= artificial fragments. '88= 1988 data, '12= 2012 data.

Surprisingly, the difference between the mainland regression slope and that of the natural islands is no longer significant, as it was in 1988. This could however be due to the fact that the current post-fire vegetation age in the mainland sites differed from that in 1988, and therefore the nature of the current vegetation communities will also differ to the historic (Bond et al., 1992). Two of the three mainland series contained relatively old growth fynbos in the smaller plot sizes and only one had young, species rich growth. The observed change in the mainland regression slope may be attributed to the the influence of different post-fire vegetation age groups in the differently sized sites. Because these changes in richness occur throughout the fire cycle, the decline can be viewed as a sampling relic.

Table 3.2 – Tests for a significant difference between the slopes of two regression lines using a simple regression comparison technique: (1) between historic data (Bond et al. 1988) and recent data (2012) in the mainland patches and the natural fynbos islands; (2) between mainland and the islands for both historic and recent data; (3) between the artificial fragments, natural islands and the mainland.

	Test	1 SE	DF	*t*-value	*P*-value
1a)	$ML_{'12}/ML_{'88}$	0.019	16	1.90	> 0.050
b)	$NI_{'12}/ NI_{'88}$	0.012	7	0.32	> 0.050
2a)	$ML_{'88}/NI_{'88}$	0.028	13	7.87	< 0.0001
b)	$ML_{'12}/NI_{'12}$	0.120	6	1.81	> 0.050
3a)	$NI_{'12}/AF_{'12}$	0.130	8	2.67	< 0.050
b)	$ML_{'12}/AF_{'12}$	0.054	16	2.40	< 0.050

ML= mainland, NI= natural islands, AF= artificial fragments. '88= 1988 data, '12= 2012 data.

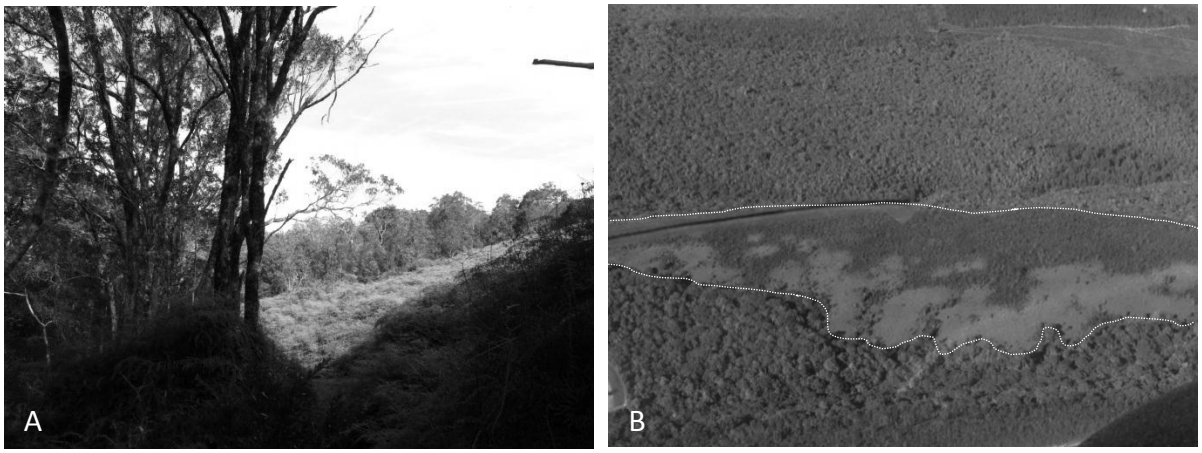

Figure 3.3 – The extent of *G. polypodioides* dominance on "NI037". (A) taken from ground-level at the fynbos-forest ecotone, and (B) taken from the air where the ecotone is represented by the dashed line. Areas of *G. polypodioides* dominance can be seen as lighter grey in (B) while areas where forest pioneer species have emerged or where tall fynbos shrubs have persisted appear darker within the fynbos island.

Data concerning the overall species richness in the natural system of mainland and naturally isolated fynbos patches reveals little deviation between 1988 and the present (Figure 3.2.A). A similar story is told by the species traits (Table 3.3.A and B). Two species traits found to deviate significantly in their frequencies between the mainland and the natural island communities in 1988 were growth form and shrub height (Bond et al. 1988). These trait frequencies are expected to shift in response to changing fire regimes, with fire dependant species becoming over-represented wherever the regime is fynbos-typical, and fire intolerant species becoming over-represented where the fire interval is prolonged. In 1988 it was found that the frequencies of growth forms differed significantly between the islands and the mainland, with graminoids being over-represented and the somewhat fire dependant geophytes under-represented (Table 3.3.Ai, from Bond et al. (1988)). The current data deviates from those findings, showing that there is now no significant difference between the growth form frequency distribution in the mainland and the natural islands (Table 3.3.Aii). However, a notable trend is that shrubs are still under-represented in both the small and large fynbos islands while the graminoids are still slightly over-represented. The small natural islands do not deviate significantly from the mainland – consistent with the 1988 findings. The growth form frequency distribution on the natural islands and the small natural islands showed no significant deviation since 1988 (Table 3.3.Aiii) indicating stability.

A similar pattern can be seen in the distribution of shrub height classes in the natural islands between 1988 and 2012 (Table 3.3.Biii) which has not changed significantly over the past 24 years. There is still a significantly different shrub height frequency distribution between the small natural islands and the mainland (Table 3.3.Bi and ii). Tall shrubs remain over-represented in these small islands while short shrubs are still under-represented. This consistency is less pronounced in the large natural islands which no longer display a significantly different distribution to the mainland (Table 3.3.Bii).

The data used to investigate the frequency distributions of these two traits concerned only fynbos-typical species, while species typical of forest and other communities were omitted from the tests.

Table 3.3 – Results from modified Chi-squared tests of the distribution of selected species traits amongst the mainland, natural islands, and artificial fragments. (A) and (B) are concerned with variation of growth form and shrub height frequencies respectively, while (C) concerns groups of habitat-typical species. (Ai) and (Bi) are from Bond et al. (1988). (Aii) and (Bii) are replicates of these using 2012 data. (Aii) and (Biii) compare the distribution in the natural islands over the past 24 years. (Aiv) and (Biv) look for variation between the natural and the artificial patches.

A) Growth forms (1=shrub, 2=graminoid, 3=forb, 4=geophyte)

A i)	Small NI/ML						All NI/ML				
1988	1	2	3	4	χ^2		1	2	3	4	χ^2
ML	40	11	10	8	NS		65	18	16	14	*
NI	39	15	10	5	3		59	28	18	8	9
A ii)	Small NI/ML						All NI/ML				
2012	1	2	3	4	χ^2		1	2	3	4	χ^2
ML	45	12	10	7	NS		65	14	14	10	NS
NI	40	15	11	9	2		60	16	17	10	1
A iii)	Small NI						All NI				
	1	2	3	4	χ^2		1	2	3	4	χ^2
1988	29	11	7	4	NS		54	26	16	7	NS
2012	26	8	12	5	5		60	16	17	10	5
A iv)	Small AF/ML						Small AF/NI				
2012	1	2	3	4	χ^2		1	2	3	4	χ^2
ML	102	28	23	17	NS	NI	90	34	25	20	NS
AF	104	22	23	20	2	AF	104	22	23	20	6

B) Shrub height (short < 1 m, medium=1-2 m, tall>2 m)

B i)	Small NI/ML					All NI/ML			
1988	Short	Medium	Tall	χ^2		Short	Medium	Tall	χ^2
ML	15	16	7	**		23	25	12	*
NI	7	16	16	14		14	26	19	8
B ii)	Small NI/ML					All NI/ML			
2012	Short	Medium	Tall	χ^2		Short	Medium	Tall	χ^2
ML	17	29	9	*		26	40	11	NS
NI	9	31	15	8		24	36	17	0
B iii)	Small NI					All NI			
	Short	Medium	Tall	χ^2		Short	Medium	Tall	χ^2
1988	7	16	16	NS		18	34	25	NS
2012	5	21	14	2		24	36	17	4
B iv)	Small AF/ML					Small AF/NI			
2012	Short	Medium	Tall	χ^2		Short	Medium	Tall	χ^2
ML	41	71	21	NS	NI	22	74	36	**
AF	44	62	26	3	AF	44	62	26	28

C) Vegetation habitat-types (FY= fynbos, N-FY= non fynbos, FO=forest, GT=generalist, FM=forest margin, FA+PL=farm & plantation)

C i)	Small NI/ML			Small NI/ML					
2012	FY	N-FY	χ^2	FY	FO	GT	FM	FA+PL	χ^2
ML	94	25	**	93	5	9	5	4	**
NI	70	48	29	70	13	18	10	6	32
C ii)	Small AF/ML			Small AF/ML					
2012	FY	N-FY	χ^2	FY	FO	GT	FM	FA+PL	χ^2
ML	222	58	**	221	12	21	12	11	**
AF	155	125	97	155	19	30	19	54	211
C iii)	Small AF/NI			Small AF/NI					
2012	FY	N-FY	χ^2	FY	FO	GT	FM	FA+PL	χ^2
NI	166	114	NS	166	31	43	24	14	**
AF	155	125	2	155	19	30	19	54	121

ML= mainland, NI= natural island, AF= artificial fragment.
Small patches ≤25 ha. χ^2 is Chi-square. NS= P >0.05, *=P <0.05, **=P <0.01.

3.3.3 Community response to artificial fragmentation

The artificial fragments represent the third fynbos configuration type. Despite being isolated, and in fact smaller than most of the natural islands, their plant communities are not always similar to those of the natural islands. The fynbos species richness in the artificial fragments is not significantly related to area (Table 3.1, Figure 3.4). The species-area regression line that results from the artificial fragments is significantly different to the regression line that results from the natural islands and from the mainland (Table 3.2, Figure 3.4.A and B) and it is more gradual.

Figure 3.4.A illustrates the position of the artificial fragments relative to the regression line from both the mainland and the natural islands in the species-area plot. The artificial fragments are generally situated above the natural island regression line, especially in the smallest fragments, and mostly below the mainland regression line, occupying the area in between the two lines. This area is illustrated by the grey triangle (Figure 3.4.B).

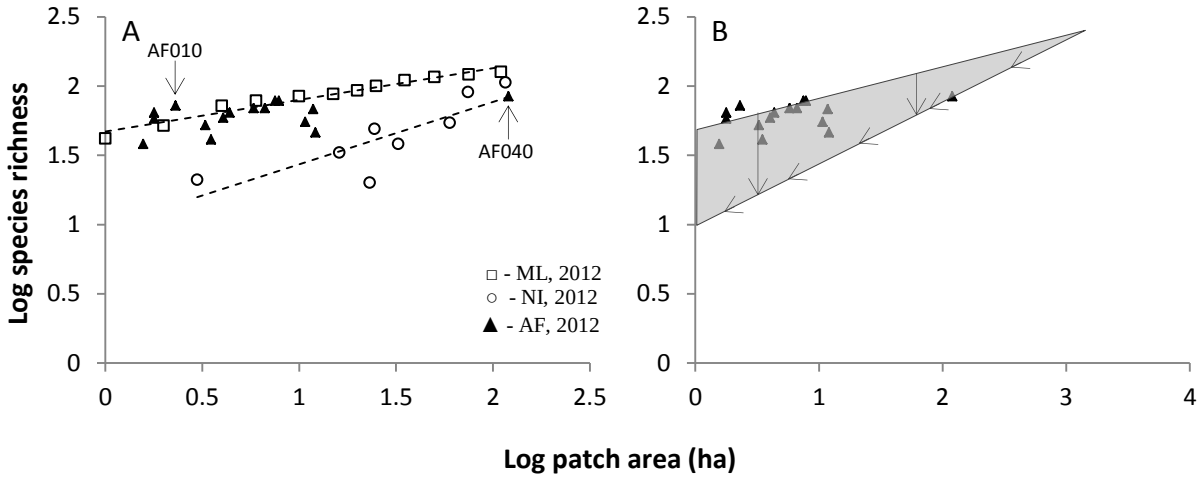

Figure 3.4 – The linear regression relationships between the fynbos species richness (log-transformed) and the area of the fynbos patch (log-transformed). ML = mainland, NI = natural islands, AF = artificial fragments. Dashed trend lines represent the current species-area relationship in the mainland and in the natural islands. (A) Compares the artificial fragments to the mainland plots and the natural islands in the species-area plot. The area of potential movement of the artificial fragments within the species-area plot is illustrated by the triangle in (D) while the arrows represent the proposed direction of movement.

The artificial fragment communities do not resemble those of the natural islands or the mainland in terms of species-area relationships, but rather they are situated somewhere between the two. Their response to fragmentation differs to that of the natural island communities when tested for the distribution of certain trait frequencies, but not for others (Table 3.3). There was no significant difference in the distribution of growth forms between the artificial fragments and the mainland or the natural islands. Although a significant difference was found between the natural islands and the mainland in 1988, my results show that growth form frequencies have not responded to fragmentation in the artificial fragments.

Shrub height distribution in the artificial islands does not deviate from that in the mainland, but is significantly different to that found in the natural islands (Table 3.3). Short shrubs are greatly over-

represented in the artificial fragments relative to the natural islands, while the medium and tall shrubs are under-represented. Short shrubs are under-represented and tall shrubs are over-represented in the natural islands relative to the mainland.

The distribution of fynbos-typical and non-fynbos-typical species in the two fragmented fynbos configuration-types differed significantly from that of the mainland (Table 3.3). Both the natural islands and the artificial fragments showed a marked under-representation of fynbos-typical species and an over-representation of non-fynbos-typical species. Compared against each other the two show no difference. The total counts of fynbos-typical species differ little between the mainland and the artificial fragments. The natural islands have fewer fynbos-typical species (122) than either the mainland (153) or the artificial fragments (157 respectively), (Figure 3.5). The distribution of habitat-typical groups differs significantly between all three of the fynbos configuration-types when the non-fynbos-typical species were placed in a single group (Table 3.3). Relative to the mainland, Fynbos-typical species are under-represented in both natural islands and artificial fragments. Relative to each other, the natural islands and artificial fragments do not differ. Farm and plantation-typical species are greatly over-represented in the artificial fragments relative to the natural islands and the mainland. Generalists, forest-typical and forest-margin typical species are all over-represented in the natural islands and the artificial fragments relative to the mainland. Forest-typical and generalist species are under-represented in the artificial fragments relative to the natural islands, while forest-margin species remain stable. Although the two isolated patch-types have similarities relative to the mainland they do differ relative to each other.

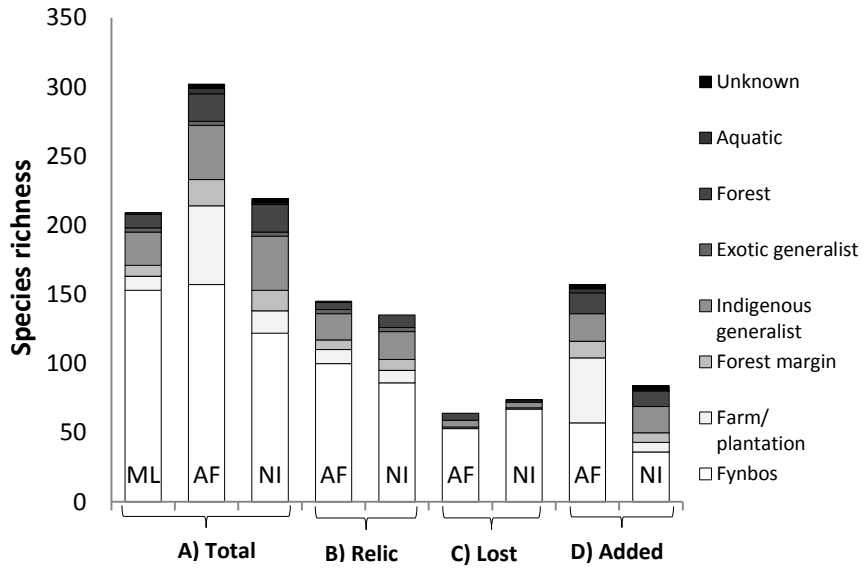

Figure 3.5 – The distribution of various habitat-typical species throughout the three fynbos configuration types. Data included total species counts. "Relic" species are those found in the isolated fynbos patches that also occur in the mainland fynbos. Similarly, "Lost" and "Added" refer to deviation in the isolated patches relative to the mainland.

The changes that have occurred in the two different isolated-community types since their isolation from the mainland have been uneven. These changes have resulted in the raised total species richness in the artificial fragments and the natural islands relative to the mainland (302 and 219 vs. 209 respectively). The artificial fragments have lost fewer species (53 vs. 67) and have retained more 'relic' species (100 vs. 86) than the natural islands (Figure 3.5.A and B). The artificial fragments also

received far more immigrant species than have the natural islands (157 vs. 84)[4], despite their more recent isolation. Much of this difference can be attributed to the farm- and plantation-typical species which have increased far more in the artificial fragments than in the natural islands (47 vs. 7). The majority of the non-fynbos 'added' species occur close to the perimeter of the patches and thus they constitute an edge effect rather than true community shift.

The artificial fragments resemble the mainland more closely than the natural islands do, at least with respect to their fynbos-typical plants. The apparent stability in the natural islands appears to present a baseline towards which the artificially fragmented communities will likely shift over time (Figure 3.4.B). The rate of this shift is unknown.

3.4 DISCUSSION

There are various reasons for the selection of small reserve-patches. In some cases, as with the artificial fragment patches of South Outeniqua Sandstone Fynbos, small isolated reserves are formed through habitat loss and are not the result of reserve planning. However there are situations in which reserve planners select a network of many small reserves for the increased metapopulation potential that this has over a network of fewer but larger reserves (Levins, 1969; Hanski & Gilpin, 1991), or where many small reserves are selected for their irreplaceability in a heterogeneous habitat. Such selections often fail to consider the full biogeographic requirements of the vegetation community inhabiting the small reserves, or the successional or cyclic nature of these communities (Pickett & Thompson, 1978). The ecological relaxation period of such communities may be far longer than expected, particularly when viewed against that of relatively short-lived faunal species.

I found that the frequency of fire in South Outeniqua Sandstone Fynbos (Rebelo et al., 2006) is positively related to the physical area of sections of this habitat. As speculated by Bond et al. (1988) and shown by studies in other ecosystems (Picket & Thompson, 1978; Wardle et al., 2003), smaller isolated fynbos patches receive fire less frequently than larger patches and mainland areas, and this drives the species-area relationship that exists in the natural islands.

I found the natural island communities to be relatively stable. Such communities are said to have reached a state of equilibrium when the rates of extinction and immigration level out (MacArthur & Wilson, 1963, 1967). In this case immigration is effectively absent considering that the natural islands, although often separated by only a few hundred meters, have a high degree of isolation when surrounded by non-fire adapted indigenous forest (van Wilgen et al., 1990; Luger & Moll, 1993; Mucina & Geldenhuys, 2006). Bond et al. (1988) found that fynbos seed dispersal is confined to within the natural islands. Thus one cannot consider these isolated fynbos communities to be at equilibrium, but rather that they are at a stable level where all fire return interval–related local extinctions have occurred and any further extinctions will result from stochastic events or typical island dynamics. The persistence of most of these patches as fynbos since the early Holocene (Midgley & Bond, 1990) affirms their stability for my purpose.

The persistence of the species-area relationship in the mainland and in the natural islands since 1988 shows that the species richness in both of these community-types is stable, as is the distribution of species traits. Although there is no longer a significant difference in the distribution of growth forms between the mainland and the islands, I suspect that this was a sampling artefact due to the various post-fire vegetation ages in the re-sampled mainland. The distributions of growth forms and shrub

[4] When fynbos-typical species are excluded: 100 vs. 58 species.

heights between the natural islands alone have not changed since 1988. This indicates that the observed stability also lies with the trait groups.

Beta diversity is considered to be the turnover of species along an environmental gradient, i.e. the turnover of alpha diversity (Whittaker, 1972). The turnover of fynbos alpha diversity also occurs along a temporal gradient of niche availability (Bond et al., 1992; Thuiller et al., 2007). This turnover is dependent on stochasticity in the natural fire regime. Variation of fire intensity, season and return interval (Bond & van Wilgen, 1996) allows ecologically similar species to coexist. A study by Thuiller et al. (2007) showed that fynbos communities are typically not stable. Species-area relationships – such as those observed in this study – may persist over successive fire-return intervals; however species turnover naturally occurs between these intervals provided that there is sufficient stochasticity in the local fire regime. Because the natural islands receive consistently extended fire-return intervals it can be expected that in time species will go locally extinct (Bond et al., 1992). This should be particularly apparent in species that occupy the same ecological niche yet vary in their response to fire-return interval. Although this is not directly shown in my results, the differing growth form and shrub height frequencies observed between the mainland and the natural islands could be linked to reduced stochasticity in the natural island fire regime.

The smallest natural island sampled in 1988, "NI00", was effectively engulfed by pioneer and ornithochorous forest species and had become indistinguishable from the surrounding forest during the past 24 years. It is of no coincidence that "NI00" was the smallest island. The natural islands are usually situated on hilltops or along ridgelines – in the path of bergwind fires (Geldenhuys, 1994). The largest islands will receive the shortest fire return intervals because they present the largest target for lightning strike or bergwind-driven cinders. Smaller islands receive over-extended fire return intervals and thus gradually lose their fire-dependant, serotinous species and gain more forest pioneer and ornithochorous species (Phillips, 1927, 1931; Bond et al., 1988; Manders & Richardson, 1992; Geldenhuys, 1994). Bond and Midgley (1995) determined that fynbos species are often more flammable than other vegetation types (van Wilgen et al., 1990) in order that fire is promoted, creating the environment for which they have a competitive advantage. Because the smaller natural islands contain fewer fynbos species and more forest species than the larger islands, it is likely that the extent of a fire would be reduced and over successive fire-return intervals the island may shrink. The island species-area curve would thus represent the stable rate of declining species richness, as represented by Figure 3.4.B. It is likely that very small islands such as "NI00" are transitional in that they will alternate between species-poor fynbos and young-growth forest due to the long and sporadic fire return interval that they receive (C. J. Geldenhuys, 2012, personal communication, August 24). This assumption requires that some fynbos species present are capable of persisting for long periods as soil-stored seeds or as shade-tolerant plants.

The role of *G. polypodioides* in the system is little understood. The fern has been found to dominate the post-fire environment in the forest and also in some of the natural islands, where it supresses the recruitment of either forest or fynbos species (Phillips, 1931). It forms thick mats that can persist for up to 70 years and only decline with the formation of a forest canopy. Certain shade tolerant resprouters that may persist after a fire are the only species capable of forming such a canopy. When the fern is burned a thick layer of charcoal and ash persists for years (J Britton, 2009, personal communication, December 15) before pioneer species can establish. Many fynbos species will be lost from a natural island under such conditions, particularly if the whole island is dominated by *G. polypodioides* as is the case in "NI037". Considering that local extinction of fynbos species on a natural island can hardly be reverted through immigration, I conclude that the dominance of *G. polypodioides* will cause a community shift towards indigenous forest.

The age of the artificial fragments is not precisely known, however they mostly originated with the afforestation of areas of fynbos 80 to 150 years ago (Filmalter & O'Keeffe, 1997; Russell et al., 2009). One might expect the vegetation communities in these fragments to have lost fynbos species during this long period of isolation and perhaps to exhibit a stable species-area relationship similar to that in the natural islands. However, there is no clear species-area relationship observed in the artificial fragments, and the resulting species-area regression curve is significantly different to both the mainland and the natural island regression curves. Artificial fragments in the species-area plot were situated below the mainland regression curve and above the natural island regression curve indicating the possibility that the fragments are still undergoing ecological relaxation (Diamond, 1972; Hylander & Ehrlén, 2013). Indeed, they accommodate more remnant fynbos-typical species than the natural islands. Therefore a relatively large extinction debt remains in the artificial fragments. The magnitude of the debt is equal to the distance between the mainland species-area curve and the natural island species-area curve at any point on the x-axis (Kuussaari et al., 2009). A larger fragment (such as "AF040") will thus hold less debt than a smaller fragment (such as "AF010"). This quantification assumes the equilibrium observed in the mainland and natural island communities.

The distribution of functional traits in the artificial fragment communities has a greater resemblance to that in the mainland than of that in the natural islands. The distribution of growth forms appears to be constant between all three fynbos configuration-types, but the natural islands stand alone in their shrub height distribution relative to the mainland and the artificial fragments. It is likely that the extinction debt lies with certain functional trait groups more than others and that short shrubs will be lost more readily than medium height or tall shrubs (Hylander & Ehrlén, 2013).The management of the artificial fynbos fragments can therefore look to the natural islands that have been naturally isolated for many years as 'models' which demonstrate the size and nature of the extinction debt in the fragments. In the case of South Outeniqua Sandstone Fynbos thousands of years of isolation (Midgley & Bond, 1990) were sufficient (probably over-sufficient) to bring the island communities to a new stable state. In other ecosystems it is important to consider whether communities of the vegetation type in question are characterised by long-term patterns such as community succession (Horn, 1975) or regeneration cycles, as are fynbos communities when using species-area relationships to determine minimum reserve size (Pickett & Thompson, 1978). If land-acquisition is limited by resources (Leader-Williams & Albon, 1988; Pressey et al., 1993; James et al., 1999; Balmford & Whitten, 2003) or if the "Several Small" reserve network is chosen for other conservation reasons, identification of extinction debt in small habitat patches can help in the decision of minimum patch size and of how to manage patches that are smaller than this.

One must consider that artificial fragments are surrounded by a novel landscape matrix, unique to each fragment; these adjacent matrices provide opportunities for novel species to invade (Wiser et al., 1998; Ewers & Didham, 2006). These species and the management thereof may increase or decrease the fire return interval and alter fire intensity in the fragments and in the surrounding matrix (Kruger, 1979; van Wilgen & Richardson, 1985; Vitousek, 1990) from where fire can spread (Gascon et al., 2000; Laurance, 2008). In this study artificial fragments received nearly twice as many non-fynbos species than the natural islands despite their relatively recent isolation. The majority of these species are generalists and those typical of agricultural and silvicultural land. Although these species are predominantly situated around the fragment edge and do not always constitute true community shift, their influence on the fire regime in the fragment must be considered. Additionally there is a sharp increase in fires of human origin and of larger natural fires in the study area (Kraaij et al., 2012). For a particular fragment, the extinction debt may not lie solely with the fire-dependant species but rather with those species most threatened by the pressures associated with that fragment's matrix.

I recommend the active removal of invasive species from the fragments and also controlling for edge and matrix effects that could interfere with long-term patterns in the vegetation community. In the case of this study, the prescription of fire should be used in the artificial fragments. However, it should be used at a conservative fire return interval in order to allow for unplanned, natural or accidental fires without jeopardising the fynbos community. The implications of prescribed burning of a fragment on neighbouring land uses should also be considered.

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Appendix 3.A – Physical characteristics of the natural islands included in the study. Sites were given unique codes that are used by SANParks. All site codes were given the prefix "NI" indicating that these areas are natural islands. Isolation distance (DTN-FY) is measured as the distance from the centre of an island to the edge of the nearest section of mainland fynbos. Post fire age categories are as follows: 1 = burnt within past 10 years; 2 = last burned between 10 and twenty years ago; 3 = has not burned in over 20 years. The specific years in which the natural island was sampled (1988 and/or 2012) are given in the final column.

Site code	Area (Ha)	DTN-FY (m)	Post fire age	Year of sampling
NI018	2.98	112	3	1988 & 2012
NI019	2.79	120	3	1988 & 2012
NI022	5.33	622	3	2012
NI035W	0.98	211	3	2012
NI036	10.72	328	3	2012
NI037	23.18	374	3	1988 & 2012
NI039	680.69	-	1	1988 & 2012
NI041	70.52	426	3	1988
NI042	24.54	744	3	1988 & 2012
NI043	13.50	218	3	2012
NI044	52.63	754	1	2012
NI047	59.82	1329	2	1988 & 2012
NI048	16.15	301	3	1988 & 2012
NI050	74.34	496	3	2012
NI064	32.52	290	3	1988 & 2012
NI067	24.60	460	3	2012

Appendix 3.B – Physical characteristics of the artificial fragments included in the study. Sites were given unique codes or codes that are used by SANParks. All site codes were given the prefix "AF" indicating that these areas are artificial fragments. Matrix heterogeneity refers to the number of discrete matrix types that border a fragment. Edge percent of "FO" (indigenous forest), "FA" (farmland), and "PL" (plantation and invasive alien trees) indicates the proportion of a fragment's perimeter that is shared with each of these three matrix types. Post-fire age group refers to one of the three post-fire age categories for fynbos vegetation.

Site code	Area (ha)	Isolation (m)	Matrix-heterogeneity	Edge-FO (%)	Edge-FA (%)	Edge-PL (%)	Post-fire age group
AF010	2.30	3922	3	53.01	3.07	43.92	3
AF011	7.51	3531	2	56.70	0.00	43.30	3
AF014	7.85	6653	3	76.59	16.46	6.96	3
AF015	6.65	7082	2	75.02	0.00	24.98	3
AF016	3.51	7888	2	54.22	0.00	45.78	3
AF032E	3.28	5773	2	63.92	0.00	14.40	2
AF032W	4.05	6193	2	37.92	39.56	0.00	3
AF033E	10.74	6259	1	86.70	0.00	0.00	2
AF033W	11.80	6510	2	85.99	0.00	0.00	3
AF040	119.99	573	2	45.26	0.00	54.74	1
AFCW	4.38	6541	2	94.85	0.00	5.15	3
AFQD	5.82	9785	3	19.23	63.95	0.00	3
AFTB	1.78	8222	3	68.20	7.43	24.37	3
AFTD	1.80	8044	2	0.00	3.41	96.59	3
AFTP	1.57	6430	3	0.00	51.69	16.10	3
AFYW	12.13	5630	3	70.79	24.85	4.36	2

Appendix 3.C – List of vegetation species recorded in this study and in 1988. Plants are recorded by family, genus and species where possible. "Community" refers to whether a species is fynbos-typical or matrix-typical. Growth forms are abbreviated as follows: AH – annual herb; DTC – deciduous tree, canopy; EPI – epiphyte; ETC – evergreen tree, canopy; ETU – evergreen tree, understory; FER – fern; GEO – geophyte; GRA – graminoid; HV – herbaceous vine; LEP – low epiphytic parasite; LES – low evergreen shrub; MEP – medium evergreen parasite; MES – medium evergreen shrub; PH – perennial herb; PHP – perennial herb parasite; SS – succulent shrub; UK – unknown; WV – woody vine. Approximate plant heights are as follows: Short (S) = 0 m -5 m; Medium (M) > 5 m -10 m; Tall (T) > 10 m. "Data" refers to the sampling year in which each species was recorded. Note that species recorded on both occasions are marked as 2012 data.

Family	Genus	Species	Comm-unity	Growth form	Height	Data
AMARYLLIDACEAE	*Cyrtanthus*	*elatus*	Fynbos	GEO	S	2012
ANACARDIACEAE	*Laurophyllus*	*capensis*	Fynbos	ETU	T	2012
ANACARDIACEAE	*Searsia*	*chirindensis*	Matrix	ETC	T	2012
ANACARDIACEAE	*Searsia*	*glauca*	Matrix	LES	S	1988
ANACARDIACEAE	*Searsia*	*lucida*	Fynbos	ETU	T	2012
ANACARDIACEAE	*Searsia*	*pyroides*	Matrix	ETU	T	2012
ANACARDIACEAE	*Searsia*	*Sp 1*	Matrix	LES	S	1988
ANACARDIACEAE	*Searsia*	*tomentosa*	Matrix	ETU	T	2012
APIACEAE	*Apiaci*	*hermus*	Fynbos	LES	S	1988
APIACEAE	*Centella*	*asiatica*	Fynbos	PH	S	2012
APIACEAE	*Centella*	*virgata*	Fynbos	PH	S	2012
APIACEAE	*Lichtensteinia*	*trifida*	Fynbos	LES	S	2012
APIACEAE	*Lichtensteinia*	*interrupta*	Fynbos	LES	S	2012
APIACEAE	*Notobubon*	*laevigatum*	Fynbos	MES	M	2012
APOCYNACEAE	*Vinca*	*Sp 1*	Matrix	HV	-	2012
AQUIFOLIACEAE	*Ilex*	*mitis*	Matrix	ETC	T	2012
ARACEAE	*Zantedeschia*	*aethiopica*	Fynbos	GEO	S	2012
ASCLEPIADACEAE	*Gomphocarpus*	*physocarpa*	Matrix	MES	M	2012
ASPARAGACEAE	*Asparagus*	*africanus*	Fynbos	LES	S	2012
ASPARAGACEAE	*Asparagus*	*Sp 1*	Fynbos	LES	S	2012
ASPARAGACEAE	*Asparagus*	*Sp 2*	Fynbos	MES	M	2012
ASTERACEAE	-	*Sp 1*	Fynbos	LES	S	2012
ASTERACEAE	-	*Sp 2*	Matrix	LES	S	2012
ASTERACEAE	-	*Sp 3*	Fynbos	MES	M	2012
ASTERACEAE	-	*Sp 4*	Fynbos	MES	M	2012
ASTERACEAE	-	*Sp 5*	Matrix	ETU	T	1988
ASTERACEAE	*Arctotheca*	*calendula*	Fynbos	AH	S	2012
ASTERACEAE	*Brachylaena*	*neriifolia*	Matrix	ETU	T	2012
ASTERACEAE	*Chrysanthemoides*	*monilifera*	Fynbos	MES	M	2012
ASTERACEAE	*Cirsium*	*vulgare*	Matrix	AH	S	2012
ASTERACEAE	*Conyza*	*sumatrensis*	Matrix	MES	M	2012
ASTERACEAE	*Corymbium*	*glabrum*	Fynbos	LES	S	2012
ASTERACEAE	*Euryops*	*virgineus*	Fynbos	MES	M	2012
ASTERACEAE	*Gerbera*	*serrata*	Fynbos	LES	S	2012
ASTERACEAE	*Helichrysum*	*cymosum*	Fynbos	PH	S	2012
ASTERACEAE	*Helichrysum*	*nudifolium*	Fynbos	LES	S	2012
ASTERACEAE	*Helichrysum*	*petiolare*	Fynbos	MES	M	2012
ASTERACEAE	*Helichrysum*	*Sp 1*	Fynbos	LES	S	2012
ASTERACEAE	*Helichrysum*	*Sp 2*	Fynbos	LES	S	2012

ASTERACEAE	*Helichrysum*	*Sp 3*	Fynbos	LES	S	2012
ASTERACEAE	*Helichrysum*	*Sp 4*	Fynbos	LES	S	2012
ASTERACEAE	*Helichrysum*	*Sp 5*	Fynbos	LES	S	2012
ASTERACEAE	*Helichrysum*	*Sp 6*	Fynbos	PH	S	2012
ASTERACEAE	*Helichrysum*	*felinum*	Fynbos	PH	S	2012
ASTERACEAE	*Helichrysum*	*foetidum*	Fynbos	MES	M	2012
ASTERACEAE	*Hippia*	*frutescens*	Fynbos	PH	S	2012
ASTERACEAE	*Hypochaeris*	*radicata*	Matrix	AH	S	2012
ASTERACEAE	*Lactuca*	*serriola*	Matrix	AH	S	2012
ASTERACEAE	*Mairia*	*crenata*	Fynbos	PH	S	2012
ASTERACEAE	*Metalasia*	*densa*	Fynbos	MES	M	2012
ASTERACEAE	*Metalasia*	*gnaphaloides*	Fynbos	MES	M	1988
ASTERACEAE	*Metalasia*	*pulcherrima*	Fynbos	LES	S	2012
ASTERACEAE	*Metalasia*	*pungens*	Fynbos	MES	M	2012
ASTERACEAE	*Osmitopsis*	*osmitoides*	Fynbos	LES	S	1988
ASTERACEAE	*Osteospermum*	*corymbosum*	Fynbos	MES	M	2012
ASTERACEAE	*Osteospermum*	*junceum*	Fynbos	EPI	S	1988
ASTERACEAE	*Osteospermum*	*polygaloides*	Fynbos	MES	M	1988
ASTERACEAE	*Othonna*	*parviflora*	Fynbos	MES	M	2012
ASTERACEAE	*Plecostachys*	*serpyllifolia*	Fynbos	PH	S	2012
ASTERACEAE	*Plecostachys*	*polifolia*	Fynbos	LES	S	1988
ASTERACEAE	*Relhania*	*calycina*	Fynbos	MES	M	2012
ASTERACEAE	*Schistostephium*	*umbellatum*	Fynbos	MES	M	2012
ASTERACEAE	*Senecio*	*angulatus*	Fynbos	LES	S	2012
ASTERACEAE	*Senecio*	*glastifolius*	Fynbos	LES	S	2012
ASTERACEAE	*Senecio*	*ilicifolius*	Matrix	LES	S	2012
ASTERACEAE	*Senecio*	*lineatus*	Fynbos	LES	S	2012
ASTERACEAE	*Senecio*	*purpureus*	Fynbos	LES	S	2012
ASTERACEAE	*Senecio*	*Sp 1*	Fynbos	MES	M	2012
ASTERACEAE	*Senecio*	*Sp 2*	Fynbos	MES	M	2012
ASTERACEAE	*Senecio*	*Sp 3*	Fynbos	MES	M	2012
ASTERACEAE	*Senecio*	*Sp 4*	Matrix	MES	M	1988
ASTERACEAE	*Senecio*	*crenatus*	Fynbos	LES	S	2012
ASTERACEAE	*Senecio*	*juniperinus*	Fynbos	MES	M	1988
ASTERACEAE	*Sonchus*	*oleraceus*	Matrix	AH	S	2012
ASTERACEAE	*Stoebe*	*alopecuroides*	Fynbos	MES	M	2012
ASTERACEAE	*Stoebe*	*plumosa*	Fynbos	LES	S	2012
ASTERACEAE	*Syncarpha*	*eximia*	Fynbos	MES	M	2012
ASTERACEAE	*Syncarpha*	*paniculata*	Fynbos	LES	S	2012
ASTERACEAE	*Syncarpha*	*paniculata*	Fynbos	LES	S	1988
ASTERACEAE	*Taraxacum*	*officinale*	Matrix	PH	S	2012
ASTERACEAE	*Tarchonanthus*	*littoralis*	Fynbos	ETU	T	2012
ASTERACEAE	*Ursinia*	*anethoides*	Fynbos	ETU	T	1988
ASTERACEAE	*Ursinia*	*chrysanthemoides*	Fynbos	AH	S	1988
ASTERACEAE	*Ursinia*	*paleacea*	Fynbos	LES	S	2012
ASTERACEAE	*Ursinia*	*trifida*	Fynbos	LES	S	1988
BLECHNACEAE	*Blechnum*	*capense*	Matrix	FER	S	1988

BLECHNACEAE	*Blechnum*	*punctulatum*	Matrix	FER	S	1988
BLECHNACEAE	*Blechnum*	*Sp 1*	Fynbos	FER	S	2012
BLECHNACEAE	*Blechnum*	*tabulare*	Fynbos	FER	S	2012
BRASSICACEAE	*Raphanus*	*raphanistrum*	Matrix	AH	S	2012
BRUNIACEAE	*Berzelia*	*intermedia*	Fynbos	MES	M	2012
BRUNIACEAE	*Brunia*	*noduliflora*	Fynbos	MES	M	2012
BUDDLEJACEAE	*Buddleja*	*salviifolia*	Fynbos	ETU	T	2012
BUDDLEJACEAE	*Nuxia*	*floribunda*	Matrix	ETC	T	2012
CANNACEAE	*Canna*	*X generalis*	Matrix	MES	M	2012
CARYOPHYLLALES	*Stellaria*	*media*	Matrix	AH	S	2012
CELASTRACEAE	*Cassine*	*schinoides*	Fynbos	ETC	T	2012
CELASTRACEAE	*Cassine*	*parvifolia*	Fynbos	ETU	T	2012
CELASTRACEAE	*Elaeodendron*	*croceum*	Fynbos	ETC	T	2012
CELASTRACEAE	*Gymnosporia*	*nemorosa*	Matrix	ETU	T	2012
CELASTRACEAE	*Maytenus*	*acuminata*	Fynbos	ETU	T	2012
CELASTRACEAE	*Maytenus*	*oleoides*	Fynbos	ETU	T	1988
CELASTRACEAE	*Pterocelastrus*	*tricuspidatus*	Fynbos	ETC	T	2012
CELASTRACEAE	*Robsonodendron*	*eucleiforme*	Fynbos	ETC	T	1988
COLCHICACEAE	*Colchicum*	*eucomoides*	Fynbos	GEO	S	2012
CONVOLVULACEAE	*Cuscuta*	*cassytoides*	Fynbos	ETU	T	2012
CORNACEAE	*Curtisia*	*dentata*	Matrix	ETC	T	2012
CRASSULACEAE	-	*Sp 1*	Fynbos	FSS	S	2012
CRASSULACEAE	*Crassula*	*fallax*	Fynbos	FSS	S	2012
CUNONIACEAE	*Cunonia*	*capensis*	Matrix	ETC	T	2012
CUPPRESSACEAE	*Widdringtonia*	*nodiflora*	Fynbos	ETU	T	2012
CYATHEACEAE	*Cyathea*	*capensis*	Matrix	FER	M	1988
CYPERACEAE	-	*Sp 1*	Fynbos	GRA	S	2012
CYPERACEAE	-	*Sp 2*	Matrix	GRA	S	2012
CYPERACEAE	-	*Sp 3*	Matrix	GRA	S	2012
CYPERACEAE	-	*Sp 4*	Fynbos	GRA	S	2012
CYPERACEAE	-	*Sp 5*	Fynbos	GRA	S	2012
CYPERACEAE	-	*Sp 6*	Fynbos	GRA	S	2012
CYPERACEAE	*Carpha*	*glomerata*	Fynbos	GRA	M	2012
CYPERACEAE	*Chrysothrix*	*capensis*	Fynbos	GRA	S	1988
CYPERACEAE	*Costularia*	*brevicaulis*	Fynbos	GRA	S	1988
CYPERACEAE	*Cyperus*	*rotundus*	Matrix	GRA	S	2012
CYPERACEAE	*Epischoenus*	*adnatus*	Fynbos	GRA	S	1988
CYPERACEAE	*Ficinia*	*nigrescens*	Fynbos	GRA	S	1988
CYPERACEAE	*Juncus*	*lomatophyllus*	Matrix	GRA	S	2012
CYPERACEAE	*Schoenoxiphium*	*altum*	Fynbos	GRA	M	2012
CYPERACEAE	*Tetraria*	*ustulata*	Fynbos	GRA	S	1988
CYPERACEAE	*Tetraria*	*compar*	Fynbos	GRA	S	1988
CYPERACEAE	*Tetraria*	*cuspidata*	Fynbos	GRA	S	1988
CYPERACEAE	*Tetraria*	*exilis*	Fynbos	GRA	S	1988
CYPERACEAE	*Tetraria*	*fimbriolata*	Fynbos	GRA	S	1988
CYPERACEAE	*Tetraria*	*involucrata*	Fynbos	GRA	S	1988
CYPERACEAE	*Tetraria*	*Sp 1*	Fynbos	GRA	M	2012

CYPERACEAE	*Tetraria*	*Sp 2*	Fynbos	GRA	M	2012
CYPERACEAE	*Tetraria*	*Sp 3*	Fynbos	GRA	S	2012
CYPERACEAE	*Tetraria*	*Sp 4*	Fynbos	GRA	S	2012
DENNSTAEDTIACEAE	*Pteridium*	*aquilinum*	Fynbos	FER	S	2012
DIOSCOREACEAE	*Dioscorea*	*sylvatica*	Matrix	HV	-	2012
DROSERACEAE	*Drosera*	*aliciae*	Matrix	PH	S	2012
EBENACEAE	*Diospyros*	*austro-africana*	Fynbos	ETU	T	1988
EBENACEAE	*Diospyros*	*dichrophylla*	Fynbos	ETC	T	2012
EBENACEAE	*Diospyros*	*glabra*	Fynbos	MES	M	2012
EBENACEAE	*Euclea*	*crispa*	Fynbos	ETC	T	2012
EBENACEAE	*Euclea*	*natalensis*	Fynbos	ETU	T	2012
EBENACEAE	*Euclea*	*racemosa*	Fynbos	ETU	T	2012
ERICACEAE	*Erica*	*canaliculata*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*cerinthoides*	Fynbos	LES	S	2012
ERICACEAE	*Erica*	*copiosa*	Fynbos	MES	M	1988
ERICACEAE	*Erica*	*cordata*	Fynbos	LES	S	2012
ERICACEAE	*Erica*	*curviflora*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*densifolia*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*discolor*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*formosa*	Fynbos	LES	S	1988
ERICACEAE	*Erica*	*formosa*	Fynbos	LES	S	2012
ERICACEAE	*Erica*	*fuscescens*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*hispidula*	Fynbos	MES	M	1988
ERICACEAE	*Erica*	*lanata*	Fynbos	LES	S	2012
ERICACEAE	*Erica*	*nabea*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*onusta*	Fynbos	LES	S	1988
ERICACEAE	*Erica*	*peltata*	Fynbos	MES	M	1988
ERICACEAE	*Erica*	*scabriuscula*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*seriphiifolia*	Fynbos	LES	S	1988
ERICACEAE	*Erica*	*sessiliflora*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*sp 1*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*sp 2*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*sp 3*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*sparsa*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*tetragona*	Fynbos	LES	S	2012
ERICACEAE	*Erica*	*uberiflora*	Fynbos	MES	M	2012
ERICACEAE	*Erica*	*glomiflora*	Fynbos	LES	S	2012
ERICACEAE	*Erica*	*cubica*	Fynbos	LES	S	2012
ERICACEAE	*Erica*	*versicolor*	Fynbos	MES	M	1988
ERIOSPERMACEAE	*Eriospermum*	*Sp 1*	Fynbos	GEO	S	1988
EUPHORBIACEAE	-	*Sp 1*	Fynbos	MES	M	2012
EUPHORBIACEAE	*Andrachne*	*ovalis*	Matrix	ETU	T	2012
EUPHORBIACEAE	*Clutia*	*affinis*	Fynbos	ETU	T	2012
EUPHORBIACEAE	*Clutia*	*alaternoides*	Fynbos	LES	S	2012
EUPHORBIACEAE	*Clutia*	*ericoides*	Fynbos	LES	S	2012
EUPHORBIACEAE	*Clutia*	*pulchella*	Fynbos	MES	M	2012
FABACEAE	-	*Sp 1*	Fynbos	MES	M	2012

FABACEAE	-	*Sp 2*	Fynbos	HV	-	2012
FABACEAE	*Acacia*	*cyclops*	Matrix	ETU	T	2012
FABACEAE	*Acacia*	*melanoxylon*	Matrix	ETC	T	2012
FABACEAE	*Amphithalea*	*fourcadei*	Fynbos	MES	M	2012
FABACEAE	*Argyrolobium*	*Amphithalea*	Fynbos	LES	S	1988
FABACEAE	*Argyrolobium*	*Sp 1*	Fynbos	LES	S	1988
FABACEAE	*Aspalathus*	*alopecurus*	Fynbos	LES	S	2012
FABACEAE	*Aspalathus*	*bowieana*	Fynbos	MES	M	2012
FABACEAE	*Aspalathus*	*kougaensis*	Fynbos	LES	S	2012
FABACEAE	*Aspalathus*	*laricifolia*	Fynbos	LES	S	2012
FABACEAE	*Aspalathus*	*rubens*	Fynbos	LES	S	1988
FABACEAE	*Aspalathus*	*sceptrum - aureum*	Fynbos	MES	M	1988
FABACEAE	*Aspalathus*	*setacea*	Fynbos	LES	S	2012
FABACEAE	*Aspalathus*	*shawii*	Fynbos	MES	M	2012
FABACEAE	*Aspalathus*	*Sp 1*	Fynbos	LES	S	2012
FABACEAE	*Aspalathus*	*Sp 2*	Fynbos	LES	S	1988
FABACEAE	*Aspalathus*	*Sp 3*	Fynbos	LES	S	1988
FABACEAE	*Aspalathus*	*Sp 4*	Fynbos	MES	M	1988
FABACEAE	*Aspalathus*	*Sp 5*	Fynbos	MES	M	1988
FABACEAE	*Cyclopia*	*subternata*	Fynbos	MES	M	2012
FABACEAE	*Dipogon*	*lignosus*	Matrix	WV	-	2012
FABACEAE	*Hypocalyptus*	*coluteoides*	Fynbos	MES	M	2012
FABACEAE	*Hypocalyptus*	*oxalidifolius*	Fynbos	LES	S	2012
FABACEAE	*Indigofera*	*alopecuroides*	Fynbos	LES	S	2012
FABACEAE	*Indigofera*	*flabellata*	Fynbos	MES	M	2012
FABACEAE	*Indigofera*	*Sp 1*	Fynbos	LES	S	2012
FABACEAE	*Indigofera*	*Sp 2*	Fynbos	LES	S	2012
FABACEAE	*Indigofera*	*stricta*	Fynbos	MES	M	2012
FABACEAE	*Indigofera*	*sulcata*	Fynbos	LES	S	2012
FABACEAE	*Lebeckia*	*meyeriana*	Fynbos	LES	S	1988
FABACEAE	*Liparia*	*hirsuta*	Fynbos	MES	M	2012
FABACEAE	*Lotus*	*subbiflorus*	Matrix	AH	S	2012
FABACEAE	*Medicago*	*Sp 1*	Matrix	PH	S	2012
FABACEAE	*Otholobium*	*prodiens*	Fynbos	MES	M	2012
FABACEAE	*Otholobium*	*sericeum*	Fynbos	MES	M	2012
FABACEAE	*Podalyria*	*myrtillifolia*	Fynbos	MES	M	2012
FABACEAE	*Podalyria*	*burchellii*	Fynbos	MES	M	2012
FABACEAE	*Psoralea*	*affinis*	Fynbos	ETU	T	2012
FABACEAE	*Psoralea*	*monophylla*	Fynbos	LES	S	1988
FABACEAE	*Psoralea*	*pinnata*	Fynbos	ETU	T	1988
FABACEAE	*Psoralea*	*plauta*	Fynbos	PH	S	2012
FABACEAE	*Rhynchosia*	*ciliata*	Fynbos	LES	S	1988
FABACEAE	*Rhynchosia*	*leucoscias*	Fynbos	LES	S	2012
FABACEAE	*Trifolium*	*Sp 1*	Matrix	PH	S	2012
FABACEAE	*Vicia*	*hirsuta*	Matrix	AH	S	2012
FABACEAE	*Virgilia*	*divaricata*	Matrix	ETC	T	2012
FUMARIACEAE	*Fumaria*	*muralis*	Matrix	PH	S	2012

GENTIANACEAE	*Chironia*	*melampyrifolia*	Fynbos	PH	S	2012
GENTIANACEAE	*Chironia*	*peduncularis*	Fynbos	PH	S	2012
GENTIANACEAE	*Sebaea*	*aurea*	Fynbos	AH	S	1988
GERANIACEAE	*Pelargonium*	*capitatum*	Fynbos	MES	M	2012
GERANIACEAE	*Pelargonium*	*cordifolium*	Fynbos	LES	S	2012
GERANIACEAE	*Pelargonium*	*radens*	Fynbos	MES	M	1988
GLEICHENIACEAE	*Gleichenia*	*polypodioides*	Fynbos	HV	-	2012
HAEMODORACEAE	*Wachendorfia*	*thyrsiflora*	Fynbos	GEO	M	2012
HEMEROCALLIDACEAE	*Caesia*	*contorta*	Fynbos	GEO	S	2012
HYACINTHACEAE	*Massonia*	*depressa*	Fynbos	GEO	S	2012
HYACINTHACEAE	*Ornithogalum*	*dubium*	Fynbos	GEO	S	2012
HYPOXIDACEAE	*Hypoxis*	*hemerocallidea*	Matrix	GEO	S	2012
ICACINACEAE	*Apodytes*	*dimidiata*	Matrix	ETU	T	1988
ICACINACEAE	*Cassinopsis*	*ilicifolia*	Matrix	ETU	T	2012
IRIDACEAE	*Aristea*	*bakeri*	Fynbos	GEO	S	2012
IRIDACEAE	*Aristea*	*pusilla*	Fynbos	GEO	S	2012
IRIDACEAE	*Aristea*	*racemosa*	Fynbos	GEO	S	2012
IRIDACEAE	*Aristea*	*spiralis*	Fynbos	GEO	S	1988
IRIDACEAE	*Bobartia*	*orientalis*	Fynbos	GEO	S	2012
IRIDACEAE	*Dietes*	*iridioides*	Fynbos	GEO	S	1988
IRIDACEAE	*Gladiolus*	*sempervirens*	Fynbos	GEO	S	1988
IRIDACEAE	*Gladiolus*	*rogersii*	Fynbos	GEO	S	2012
IRIDACEAE	*Hesperantha*	*falcata*	Fynbos	GEO	S	2012
IRIDACEAE	*Hesperantha*	*radiata*	Matrix	GEO	S	2012
IRIDACEAE	*Moraea*	*lewisiae*	Fynbos	GEO	S	2012
IRIDACEAE	*Romulea*	*rosea*	Fynbos	GEO	S	2012
IRIDACEAE	*Tritoniopsis*	*caffra*	Fynbos	GEO	S	2012
IRIDACEAE	*Watsonia*	*fourcadei*	Fynbos	GEO	S	2012
IRIDACEAE	*Watsonia*	*knysnana*	Fynbos	GEO	S	2012
IRIDACEAE	*Watsonia*	*wilmaniae*	Fynbos	GEO	S	2012
LAMIACEAE	*Stachys*	*aethiopica*	Fynbos	PH	S	2012
LAMIACEAE	*Stachys*	*ciliata*	Fynbos	PH	S	2012
LAMIACEAE	*Stachys*	*thunbergii*	Fynbos	MES	M	1988
LAURACEAE	*Cassytha*	*ciliolata*	Fynbos	HV	-	2012
LAURACEAE	*Ocotea*	*bullata*	Matrix	ETC	T	2012
LENTIBULARIACEAE	*Utricularia*	*bisquamata*	Matrix	AH	S	2012
LINACEAE	*Linum*	*africanum*	Fynbos	PH	S	2012
LOBELIACEAE	*Lobelia*	*coronopifolia*	Fynbos	PH	S	1988
LOBELIACEAE	*Lobelia*	*neglecta*	Fynbos	PH	S	2012
LOBELIACEAE	*Lobelia*	*Sp 1*	Fynbos	PH	S	2012
LOBELIACEAE	*Lobelia*	*cuneifolia*	Fynbos	PH	S	2012
LOBELIACEAE	*Lobelia*	*tomentosa*	Fynbos	PH	S	2012
LOBELIACEAE	*Monopsis*	*unidentata*	Fynbos	PH	S	2012
LYCOPODIACEAE	*Lycopodiella*	*cernuum*	Matrix	UK	S	2012
MALVACEAE	*Anisodontea*	*scabrosa*	Fynbos	MES	M	1988
MALVACEAE	*Hermannia*	*filifolia*	Fynbos	PH	S	2012
MALVACEAE	*Sparrmannia*	*africana*	Fynbos	ETU	T	2012

MENYANTHACEAE	*Villarsia*	*capensis*	Matrix	PH	S	2012
MESEMBRYANTHEMACEAE	*Carpobrotus*	*deliciosus*	Fynbos	FSS	S	2012
MESEMBRYANTHEMACEAE	*Carpobrotus*	*edulis*	Fynbos	FSS	S	2012
MIMOSACEAE	*Acacia*	*mearnsii*	Matrix	ETC	T	2012
MONTINIACEAE	*Montinia*	*caryophyllacea*	Fynbos	MES	M	2012
MYRICACEAE	*Morella*	*cordifolia*	Fynbos	ETU	T	1988
MYRICACEAE	*Morella*	*humilis*	Fynbos	LES	S	2012
MYRSINACEAE	*Myrsine*	*africana*	Fynbos	ETU	T	1988
MYRSINACEAE	*Rapanea*	*melanophloeos*	Matrix	ETC	T	2012
MYRTACEAE	*Eucalyptus*	*Sp 1*	Matrix	ETC	T	2012
OCHNACEAE	*Ochna*	*natalitia*	Matrix	MES	M	2012
OLEACEAE	*Olea*	*capensis*	Matrix	ETC	T	2012
OLEACEAE	*Olea*	*exasperata*	Fynbos	ETU	T	2012
OLINIACEAE	*Olinia*	*ventosa*	Matrix	ETC	T	2012
ORCHIDACEAE	*Angraecum*	*sacciferum*	Matrix	EPI	S	1988
ORCHIDACEAE	*Ceratandra*	*grandiflora*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Disa*	*bracteata*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Disa*	*cornuta*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Disa*	*hians*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Disa*	*racemosa*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Disa*	*sagittalis*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Disperis*	*capensis*	Fynbos	GEO	S	1988
ORCHIDACEAE	*Eulophia*	*aculeata*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Mystacidium*	*capense*	Matrix	GEO	S	1988
ORCHIDACEAE	*Satyrium*	*ligulatum*	Fynbos	GEO	S	2012
ORCHIDACEAE	*Satyrium*	*Sp 1*	Fynbos	GEO	S	1988
ORCHIDACEAE	*Satyrium*	*Sp 2*	Fynbos	GEO	S	1988
OROBANCHACEAE	*Harveya*	*capensis*	Fynbos	PHP	S	2012
OROBANCHACEAE	*Harveya*	*purpurea*	Fynbos	PHP	S	2012
OROBANCHACEAE	*Hyobanche*	*Sp 1*	Fynbos	PHP	S	1988
OROBANCHACEAE	*Melasma*	*scabrum*	Fynbos	PHP	S	2012
OXALIDACEAE	*Oxalis*	*incarnata*	Matrix	GEO	S	2012
OXALIDACEAE	*Oxalis*	*purpurea*	Fynbos	GEO	S	2012
OXALIDACEAE	*Oxalis*	*Sp 1*	Matrix	GEO	S	2012
PENAEACEAE	*Penaea*	*acutifolia*	Fynbos	MES	M	1988
PENAEACEAE	*Penaea*	*cneorum*	Fynbos	MES	M	2012
PENAEACEAE	*Penaea*	*mucronata*	Fynbos	MES	M	1988
PENAEACEAE	*Penaea*	*Sp 1*	Fynbos	MES	M	1988
PHYLLANTHACEAE	*Lachnostylis*	*hirta*	Matrix	ETU	T	2012
PINACEAE	*Pinus*	*Sp 1*	Matrix	ETC	T	2012
PLANTAGINACEAE	*Plantago*	*lanceolata*	Matrix	PH	S	2012
POACEAE	-	*Sp 1*	Fynbos	GRA	S	2012
POACEAE	-	*Sp 2*	Matrix	GRA	S	2012
POACEAE	*X Triticosecale*		Matrix	GRA	S	2012
POACEAE	*Andropogon*	*appendiculatus*	Fynbos	GRA	S	1988
POACEAE	*Avena*		Matrix	GRA	S	2012
POACEAE	*Chloris*	*virgata*	Matrix	GRA	S	2012

POACEAE	*Cynodon*	*dactylon*	Matrix	GRA	S	2012
POACEAE	*Ehrharta*	*calycina*	Fynbos	GRA	S	2012
POACEAE	*Ehrharta*	*ramosa*	Fynbos	GRA	S	1988
POACEAE	*Ehrharta*	*rehmannii*	Fynbos	GRA	S	1988
POACEAE	*Eragrostis*	*capensis*	Fynbos	GRA	S	2012
POACEAE	*Eragrostis*	*cilianensis*	Matrix	GRA	S	2012
POACEAE	*Eragrostis*	*plana*	Matrix	GRA	S	2012
POACEAE	*Heteropogon*	*contortus*	Fynbos	GRA	S	2012
POACEAE	*Lolium*	*multiflorum*	Matrix	GRA	S	2012
POACEAE	*Merxmuellera*	*decora*	Fynbos	GRA	S	1988
POACEAE	*Panicum*	*Sp 1*	Matrix	GRA	S	2012
POACEAE	*Paspalum*	*dilatatum*	Matrix	GRA	S	2012
POACEAE	*Paspalum*	*urvillei*	Matrix	GRA	S	2012
POACEAE	*Pennisetum*	*clandestinum*	Matrix	GRA	S	2012
POACEAE	*Pentaschistis*	*curvifolia*	Fynbos	GRA	S	2012
POACEAE	*Poa*	*annua*	Matrix	GRA	S	2012
POACEAE	*Sporobolus*	*africanus*	Fynbos	GRA	S	1988
POACEAE	*Stenotaphrum*	*secundatum*	Matrix	GRA	S	2012
POACEAE	*Themeda*	*triandra*	Matrix	GRA	S	2012
POACEAE	*Tribolium*	*uniolae*	Fynbos	GRA	S	2012
POACEAE	*Urochloa*	*panicoides*	Matrix	GRA	S	2012
PODOCARPACEAE	*Afrocarpus*	*falcatus*	Matrix	ETC	T	2012
PODOCARPACEAE	*Podocarpus*	*latifolius*	Matrix	ETC	T	2012
POLYGALACEAE	*Muraltia*	*ericaefolia*	Fynbos	PH	S	2012
POLYGALACEAE	*Muraltia*	*satureioides*	Fynbos	LES	S	2012
POLYGALACEAE	*Muraltia*	*Sp 1*	Fynbos	LES	S	2012
POLYGALACEAE	*Muraltia*	*ericoides*	Fynbos	LES	S	1988
POLYGALACEAE	*Podalyria*	*Sp 1*	Fynbos	LES	S	2012
POLYGALACEAE	*Polygala*	*bracteolata*	Fynbos	LES	S	1988
POLYGALACEAE	*Polygala*	*ericaefolia*	Fynbos	LES	S	1988
POLYGALACEAE	*Polygala*	*fruticosa*	Fynbos	MES	M	2012
POLYGALACEAE	*Polygala*	*myrtifolia*	Fynbos	MES	M	2012
POLYGALACEAE	*Polygala*	*peduncularis*	Fynbos	MES	M	2012
POLYGALACEAE	*Polygala*	*Sp 1*	Fynbos	LES	S	2012
POLYGALACEAE	*Polygala*	*garcinii*	Fynbos	LES	S	2012
POLYGONACEAE	*Polygonum*	*aviculare*	Matrix	AH	S	2012
POLYGONACEAE	*Rumex*	*crispus*	Matrix	LES	S	2012
PRIMULACEAE	*Anagallis*	*arvensis*	Matrix	AH	S	2012
PROTEACEAE	*Hakea*	*sericea*	Matrix	MES	M	2012
PROTEACEAE	*Leucadendron*	*conicum*	Fynbos	ETU	T	2012
PROTEACEAE	*Leucadendron*	*eucalyptifolium*	Fynbos	ETU	T	2012
PROTEACEAE	*Leucadendron*	*salignum*	Fynbos	MES	M	2012
PROTEACEAE	*Leucadendron*	*spissifolium*	Fynbos	MES	M	2012
PROTEACEAE	*Leucadendron*	*uliginosum*	Fynbos	ETU	T	2012
PROTEACEAE	*Leucospermum*	*glabrum*	Fynbos	MES	M	2012
PROTEACEAE	*Mimetes*	*pauciflorus*	Fynbos	MES	M	2012
PROTEACEAE	*Protea*	*cynaroides*	Fynbos	MES	M	2012

PROTEACEAE	*Protea*	*mundii*	Fynbos	ETU	T	2012
PROTEACEAE	*Protea*	*neriifolia*	Fynbos	ETU	T	2012
RANUNCULACEAE	*Ranunculus*	*multifidus*	Fynbos	PH	S	2012
RESTIONACEAE	-	*Sp 1*	Fynbos	GRA	S	2012
RESTIONACEAE	-	*Sp 2*	Fynbos	GRA	S	2012
RESTIONACEAE	-	*Sp 3*	Fynbos	GRA	S	2012
RESTIONACEAE	-	*Sp 4*	Fynbos	LES	S	1988
RESTIONACEAE	*Calopsis*	*membranacea*	Fynbos	GRA	S	1988
RESTIONACEAE	*Cannomois*	*virgata*	Fynbos	GRA	M	2012
RESTIONACEAE	*Elegia*	*equisetacea*	Fynbos	GRA	S	1988
RESTIONACEAE	*Elegia*	*juncea*	Fynbos	GRA	S	1988
RESTIONACEAE	*Elegia*	*Sp 1*	Fynbos	GRA	S	2012
RESTIONACEAE	*Elegia*	*Sp 2*	Fynbos	GRA	S	1988
RESTIONACEAE	*Elegia*	*thyrsoidea*	Fynbos	GRA	S	1988
RESTIONACEAE	*Elegia*	*vaginulata*	Fynbos	GRA	S	1988
RESTIONACEAE	*Elegia*	*galpinii*	Fynbos	GRA	S	1988
RESTIONACEAE	*Elegia*	*racemosa*	Fynbos	GRA	S	1988
RESTIONACEAE	*Elegia*	*fistulosa*	Fynbos	GRA	S	2012
RESTIONACEAE	*Hypodiscus*	*striatus*	Fynbos	GRA	S	1988
RESTIONACEAE	*Hypodiscus*	*synchroolepis*	Fynbos	GRA	S	1988
RESTIONACEAE	*Hypodiscus*	*Sp 1*	Fynbos	GRA	S	2012
RESTIONACEAE	*Ischyrolepis*	*leptoclados*	Fynbos	GRA	S	1988
RESTIONACEAE	*Mastersiella*	*purpurea*	Fynbos	GRA	S	2012
RESTIONACEAE	*Platycaulos*	*anceps*	Fynbos	GRA	S	1988
RESTIONACEAE	*Platycaulos*	*compressus*	Fynbos	GRA	S	1988
RESTIONACEAE	*Restio*	*fourcadei*	Fynbos	GRA	S	2012
RESTIONACEAE	*Restio*	*triticeus*	Fynbos	GRA	S	1988
RESTIONACEAE	*Rhodocoma*	*capensis*	Fynbos	GRA	S	1988
RESTIONACEAE	*Rhodocoma*	*cymosum*	Fynbos	GRA	S	1988
RESTIONACEAE	*Rhodocoma*	*gigantea*	Fynbos	GRA	M	2012
RESTIONACEAE	*Thamnochortus*	*cinereus*	Fynbos	GRA	M	2012
RESTIONACEAE	*Willdenowia*	*teres*	Fynbos	GRA	S	1988
RHAMNACEAE	*Phylica*	*imberbis*	Fynbos	LES	S	1988
RHAMNACEAE	*Phylica*	*paniculata*	Fynbos	MES	M	2012
RHAMNACEAE	*Phylica*	*pinea*	Fynbos	MES	M	2012
RHAMNACEAE	*Phylica*	*purpurea*	Fynbos	ETU	T	2012
RHAMNACEAE	*Phylica*	*Sp 1*	Fynbos	MES	M	1988
RHAMNACEAE	*Phylica*	*axillaris*	Fynbos	LES	S	2012
RHAMNACEAE	*Rhamnus*	*prinoides*	Fynbos	ETU	T	2012
RHAMNACEAE	*Scutia*	*myrtina*	Fynbos	ETU	T	1988
ROSACEAE	*Cliffortia*	*burchellii*	Fynbos	GRA	S	1988
ROSACEAE	*Cliffortia*	*exilifolia*	Fynbos	MES	M	1988
ROSACEAE	*Cliffortia*	*graminea*	Fynbos	MES	M	2012
ROSACEAE	*Cliffortia*	*odorata*	Fynbos	MES	M	2012
ROSACEAE	*Cliffortia*	*paucistaminea*	Fynbos	MES	M	2012
ROSACEAE	*Cliffortia*	*Sp 1*	Fynbos	MES	M	2012
ROSACEAE	*Cliffortia*	*Sp 2*	Fynbos	MES	M	1988

ROSACEAE	*Cliffortia*	*Sp 3*	Fynbos	MES	M	1988
ROSACEAE	*Cliffortia*	*ilicifolia*	Fynbos	MES	M	2012
ROSACEAE	*cliffortia*	*linearifolia*	Fynbos	MES	M	2012
ROSACEAE	*Cliffortia*	*stricta*	Fynbos	MES	M	2012
ROSACEAE	*Rubus*	*fruticosus*	Fynbos	MES	M	2012
ROSACEAE	*Rubus*	*rigidus*	Fynbos	MES	M	2012
RUBIACEAE	*Anthospermum*	*galioides*	Fynbos	LES	S	2012
RUBIACEAE	*Anthospermum*	*Sp 1*	Fynbos	PH	S	2012
RUBIACEAE	*Burchellia*	*bubalina*	Matrix	ETU	T	2012
RUBIACEAE	*Carpacoce*	*spermacoccea*	Fynbos	MES	M	1988
RUBIACEAE	*Galopina*	*urcaeoides*	Matrix	MES	M	1988
RUBIACEAE	*Psydrax*	*obovata*	Matrix	LES	S	1988
RUTACEAE	*Agathosma*	*capensis*	Fynbos	MEP	M	1988
RUTACEAE	*Agathosma*	*ovata*	Fynbos	ETU	T	2012
RUTACEAE	*Agathosma*	*Sp 1*	Fynbos	MES	M	2012
RUTACEAE	*Agathosma*	*cerefolium*	Fynbos	MES	M	2012
RUTACEAE	*Empleurum*	*unicapsulare*	Fynbos	MES	M	2012
SALICACEAE	*Populus*	*Sp 1*	Matrix	DTC	T	2012
SANTALACEAE	*Osyris*	*compressum*	Fynbos	MEP	M	2012
SANTALACEAE	*Thesium*	*Sp 1*	Fynbos	PHP	S	2012
SANTALACEAE	*Thesium*	*carinatum*	Fynbos	MEP	M	1988
SANTALACEAE	*Thesium*	*nigromontanum*	Fynbos	MEP	M	1988
SANTALACEAE	*Thesium*	*strictum*	Fynbos	LES	S	1988
SANTALACEAE	*Thesium*	*umbelliferum*	Fynbos	MEP	M	2012
SCHIZACEAE	*Schizaea*	*pectinata*	Fynbos	FER	S	2012
SCROPHULARIACEAE	*Diclis*	*reptans*	Matrix	PH	S	2012
SCROPHULARIACEAE	*Graderia*	*scabra*	Fynbos	PHP	S	2012
SCROPHULARIACEAE	*Halleria*	*lucida*	Fynbos	ETU	T	2012
SCROPHULARIACEAE	*Pseudoselago*	*spuria*	Fynbos	LES	S	1988
SCROPHULARIACEAE	*Selago*	*glomerata*	Fynbos	FSS	S	2012
SCROPHULARIACEAE	*Selago*	*corymbosa*	Fynbos	LES	S	2012
SCROPHULARIACEAE	*Selago*	*Sp 1*	Fynbos	MES	M	2012
SCROPHULARIACEAE	*Selago*	*Sp 2*	Fynbos	LES	S	2012
SCROPHULARIACEAE	*Sutera*	*Sp 1*	Matrix	PH	S	2012
SOLANACEAE	*Physalis*	*peruviana*	Matrix	LES	S	2012
SOLANACEAE	*Solanum*	*nigrum*	Matrix	AH	S	2012
SOLANACEAE	*Solanum*	*linnaeanum*	Matrix	LES	S	2012
SOLANACEAE	*Solanum*	*mauritianum*	Matrix	ETU	T	2012
SPARRMANNIACEAE	*Grewia*	*occidentalis*	Fynbos	ETU	T	2012
THYMELAEACEAE	*Gnidia*	*denudata*	Fynbos	MES	M	2012
THYMELAEACEAE	*Gnidia*	*francisci*	Fynbos	LES	S	1988
THYMELAEACEAE	*Gnidia*	*oppositifolia*	Fynbos	LES	S	2012
THYMELAEACEAE	*Gnidia*	*Sp 1*	Fynbos	LES	S	2012
THYMELAEACEAE	*Gnidia*	*juniperifolia*	Fynbos	MES	M	2012
THYMELAEACEAE	*Lachnaea*	*diosmoides*	Fynbos	MES	M	2012
THYMELAEACEAE	*Passerina*	*falcifolia*	Fynbos	MES	M	2012
THYMELAEACEAE	*Struthiola*	*argentea*	Fynbos	LES	S	2012

THYMELAEACEAE	*Struthiola*	*macowanii*	Fynbos	LES	S	1988
THYMELAEACEAE	*Struthiola*	*exclonii*	Fynbos	MES	M	1988
THYMELAEACEAE	*Struthiola*	*eckloniana*	Fynbos	MES	M	2012
TYPHACEAE	*Typha*	*capensis*	Matrix	GRA	M	2012
UNKNOWN	-	*Sp 1*	Fynbos	GEO	S	2012
UNKNOWN	-	*Sp 10*	Matrix	GRA	S	2012
UNKNOWN	-	*Sp 11*	Matrix	GRA	S	2012
UNKNOWN	-	*Sp 12*	Matrix	UK	S	2012
UNKNOWN	-	*Sp 13*	Matrix	ETU	T	2012
UNKNOWN	-	*Sp 14*	Matrix	ETU	T	2012
UNKNOWN	-	*Sp 15*	Matrix	PH	S	2012
UNKNOWN	-	*Sp 16*	Matrix	ETU	T	1988
UNKNOWN	-	*Sp 17*	Matrix	ETU	T	1988
UNKNOWN	-	*Sp 18*	Matrix	ETU	T	1988
UNKNOWN	-	*Sp 19*	Matrix	ETU	T	2012
UNKNOWN	-	*Sp 2*	Fynbos	ETU	T	2012
UNKNOWN	-	*Sp 20*	Matrix	HV	-	1988
UNKNOWN	-	*Sp 21*	Matrix	ETC	T	2012
UNKNOWN	-	*Sp 22*	Matrix	AH	S	2012
UNKNOWN	-	*Sp 23*	Matrix	ETU	T	2012
UNKNOWN	-	*Sp 24*	Matrix	ETU	T	2012
UNKNOWN	-	*Sp 25*	Matrix	AH	S	2012
UNKNOWN	-	*Sp 26*	Matrix	GRA	S	2012
UNKNOWN	-	*Sp 3*	Fynbos	FER	S	2012
UNKNOWN	-	*Sp 4*	Fynbos	LES	S	2012
UNKNOWN	-	*Sp 5*	Fynbos	HV	-	2012
UNKNOWN	-	*Sp 6*	Fynbos	FSS	S	2012
UNKNOWN	-	*Sp 7*	Fynbos	LES	S	2012
UNKNOWN	-	*Sp 8*	Fynbos	MES	M	1988
UNKNOWN	-	*Sp 9*	Matrix	ETU	T	2012
URTICACEAE	*Didymodoxa*	*caffra*	Matrix	AH	S	2012
URTICACEAE	*Urtica*	*urens*	Matrix	PH	S	2012
VERBENACEAE	*Chascanum*	*cernuum*	Fynbos	LES	S	1988
VERBENACEAE	*Verbena*	*bonariensis*	Matrix	MES	M	2012
VISCACEAE	*Viscum*	*capense*	Fynbos	LEP	S	2012
VISCACEAE	*Viscum*	*obscurum*	Fynbos	LEP	S	2012

CHAPTER 4: THE USE OF FYNBOS FRAGMENTS BY BIRDS: STEPPING-STONE HABITATS AND RESOURCE REFUGIA

4.1. INTRODUCTION

4.1.1 Fragmentation

Habitat loss and fragmentation pose a major threat to biodiversity globally (Saunders et al., 1991; Sala et al., 2000). Habitat fragments are characterised by reduced effective habitat area, increased isolation from neighbouring fragments and from source populations, and an increasingly human modified matrix which surrounds them (Saunders et al., 1991; Ricketts, 2001; Fahrig, 2003; Reed, 2004). These mechanisms act to isolate biotic communities that inhabit fragments and, for some species, to reduce their connectivity (Ricketts, 2001; Kieck, 2009). Many studies have explored the negative aspects of habitat fragmentation (Andrén, 1994; Fahrig, 2003; Fischer & Lindenmayer, 2007, and see Chapter 2, Section 3). Indeed, a landscape fragmented by human land-uses is by no means the optimal habitat for biodiversity. Fewer studies investigate the conservation potential of habitat fragments. Those that do have highlighted the value of fragments for conserving species diversity (Saunders et al., 1987; Turner & Corlett, 1996; Tscarntke et al., 2002; Struebig et al., 2008, and see Chapter 3). This is reassuring when one considers that fragmented landscapes have become common (Fahrig, 2003; Lindenmayer & Fischer, 2006; Kitzes & Merenlender, 2013) and include habitat fragments that vary in terms of size, degree of isolation and surrounding matrix composition.

4.1.2 Small reserves and stepping stones

Habitat loss and the biodiversity crisis (Pimm et al., 1995) have driven the establishment of reserves and protected areas. The subject of area prioritization for conservation has been highly debated in the scientific literature (see Chapter 2, Section 2.3) and many available tools can assist in the design of optimally representative reserve networks (e.g. Pressey et al., 1993; Lombard et al., 1997; Margules & Pressey, 2000; Rodrigues et al., 2000; Margules et al., 2002; Arponen et al., 2007; Moilanen & Wintle, 2007; Pressey & Bottrill, 2008). The size and arrangement of reserves in networks – brought to light through the ‘single-large or several-small reserves’ debate is the concern of many conservation ecologists (e.g. Gilpin & Diamond, 980; Terborgh, 1974; Diamond, 1975; Simberloff & Abele, 1976; Wilcox & Murphy, 1985; Ovaskainen, 2002). When designing a network of biodiversity reserves it is important for conservation agencies to use selection criteria that will complement their conservation goals (Virolainen et al., 1999; Rothley et al., 2004). With the limited resources available to them (Leader-Williams & Albon, 1988; Pressey et al., 1993; James et al., 1999; Balmford & Whitten, 2003), selections are often made through opportunism and in reality, small and isolated reserves often result. These however, often do have conservation value (Janzen, 1988; Shafer, 1995; Turner & Corlett, 1996; Struebig et al., 2008). In some cases small habitat fragments are all that is left of a habitat-type following habitat loss and fragmentation (Saunders et al., 1991; Turner & Corlett, 1996). Fragments that are the refuge of threatened taxa certainly hold conservation value. Habitat fragments have also been found to increase connectivity in reserve networks by functioning as ‘stepping-stone’ habitats, effectively linking two larger conservation areas for motile taxa and wide ranging taxa (MacArthur & Wilson, 1967; Gilpin, 1980; Fischer & Lindenmayer, 2002; 2007; Baum et al., 2004).

4.1.3 Fragmentation effects

Artificially fragmented communities are assumed to suffer from 'island effects', the extent of which depends on the nature of the species in the community (Margules et al., 1994; Dooley & Bowers, 1998; Davies et al., 2000; Henle et al., 2004; Kieck, 2009). According to island biogeography theory (MacArthur & Wilson, 1963, 1967; Whitehead & Jones, 1969; Brown & Kodric-Brown, 1977), and subsequent metapopulation theory (Hanski & Gilpin, 1991), communities on small, highly isolated habitats suffer from higher extinction rates and lower immigration rates than those on large habitats that are less isolated (see Chapter 2, Section 2.2). Therefore the rates of extinction and immigration are unique to each individual isolated habitat patch and are responsible for the equilibrium level of species richness in each patch. In sedentary insular communities, such as vegetation characterised by short-distance dispersal (See Chapter 3), the rate of immigration may be effectively zero and species richness is determined by extinction alone (Brown, 1971; Bond et al., 1988). In such cases one cannot assume that a relatively stable level of species richness is representative of an equilibrium state, but rather of a quasi-equilibrium state (see Chapter 2, Sections 2.2 and 3.7). Motile species, such as birds, have the capacity to use habitat fragments according to the principles stated in the equilibrium theory of island biogeography; their rates of immigration and local extinction constituting a true equilibrium, *ceteris paribus*. If, however some component of their habitat is non-linear – such as the temporal turnover of vegetation species in fire-adapted fynbos shrublands (Thuiller et al., 2007) – then this equilibrium level may fluctuate in a similar, non-linear manner.

The nature of the surrounding matrix and the amount of time that has elapsed since initial fragmentation both affect fragment communities in ways that are not accounted for by the equilibrium theory of island biogeography (see Chapter 2, Section 3). The human land-uses that typically surround habitat fragments can influence the effective area and isolation of a fragment for certain fragment taxa. This depends on the ability or the choice of these taxa to use the surrounding matrix as an extension of their habitat (Gascon et al., 1999; Norton et al., 2000; Brotons et al., 2003; Jules & Shahani, 2003) or to migrate across or through it when dispersing to the mainland or to other isolated habitats (Gascon et al., 1999; Ricketts, 2001; Brotons et al., 2003; Strayer et al., 2003). Thus these matrix effects depend on the nature of the fragmented biological community and on the nature of the surrounding matrix (see Chapter 2, Sections 3.2 and 3.3). The surrounding matrix can also introduce invasive species (Saunders et al., 1991; Kemper et al., 1999; Hobbs & Yates, 2003; Buckley et al., 2006; Lindenmayer & Fischer, 2006) and novel disturbances (Saunders et al., 1991; Brotons et al., 2003; Rouget et al., 2006; Kongor, 2009) to a fragment (see Chapter 2, Sections 3.4 and 3.5), as well as altering the natural disturbance regime (Bond et al., 1988; Andrén, 1994; Baker, 1994; Mack & D'Antonio, 1998; Hargrove et al., 2000) in a fragment (as seen in Chapter 3, Section 3.1).

Empirical fragmentation studies often find that local species – particularly those that are relatively motile – respond primarily to area constraints, with other factors such as isolation distance and the nature of the surrounding matrix being of lesser importance (e.g. Bender et al., 1998; Lee et al., 2002; Ferraz et al., 2007; Sekercioglu, 2007; Kieck, 2009). Species-Area curves are designed to illustrate and investigate species-area relationships and have been used to establish minimum critical reserve size (e.g. Bond et al., 1988; Cowling & Bond, 1991; Rybicki & Hanski, 2013). In this regard users are cautioned to consider the various methods of collecting species-area data because these methods may influence the apparent relationship at which they arrive (Dengler, 2009; Rybicki & Hanski, 2013). Although species-area relationships are very useful tools in habitat fragmentation studies, they should be used in conjunction with data concerning species response to other drivers of community change, such as the extent of isolation, the nature of the surrounding matrix and the amount of time elapsed since initial fragmentation.

Extinction debt is defined as the difference between the number of species present in a community at fragmentation and the number present in the community when it has reached a new, post-fragmentation (quasi-) equilibrium state (Tilman et al., 1994; Malanson, 2008; Kuussaari et al., 2009; Hylander & Ehrlén, 2013). This is usually characterised by a lag period during which ecological relaxation occurs (Diamond, 1972; Gonzalez, 2000; MacHunter et al., 2006, and see Chapter 2, Section 3.6). Extinction debt is usually associated with more recently fragmented communities. Scientists often attempt to quantify this extinction debt in order to better understand the full conservation implications of habitat fragmentation; knowledge of which species in a community are prone to time delayed extinction provides conservationists with an opportunity to intervene before these species are lost (Malanson, 2008; Jackson & Sax, 2009; Kuussaari et al., 2009; Wearn et al., 2012; Hylander & Ehrlén, 2013, and see Chapter 3). If these fragments are small, highly isolated or subject to adverse matrix effects (or a combination of these) then conservation agencies are required to manage these constraints in order to prevent local species extinctions or to achieve their specific conservation goals. When this is achievable, habitat fragments gain conservation value.

4.1.4 Fynbos biodiversity

The Cape Floristic Region is a biodiversity hotspot in South Africa (Myers et al., 2000) and contains exceptionally high botanical diversity (Goldblatt, 1978; White, 1983; Takhtajan, 1986). Fynbos is a mediterranean-type ecosystem found within this region which supports ecologically important bird species (Sala et al., 2000; Rebelo et al., 2006). Although fynbos-typical birds are less diverse than the local vegetation, certain bird species, such as the Cape Sugarbird (*Promerops cafer*) and the Orange-breasted Sunbird (*Anthobaphes violacea*) play an important role in the maintenance of the vegetation community through pollination (Bond, 1994; Hockey et al., 2005; Pauw & Louw, 2012; Chalmandrier et al., 2013).

Fragmentation by urban development, agriculture, plantation forestry and the spread of invasive alien plants threatens fynbos vegetation communities (Rouget et al., 2003; Rebelo et al., 2006) such as those in South Outeniqua Sandstone Fynbos (Rebelo et al., 2006). Although the fynbos-endemic avifauna is generally not recognised as threatened biodiversity, their conservation status is being questioned, particularly under the pressures of habitat loss and fragmentation and the proposed effect of range declines and degradation of habitat quality brought about through anthropogenic climate change (Keith et al., 2008; Huntley & Barnard, 2012; Lee & Barnard, 2012; Chalmandrier et al., 2013). Dures and Cumming (2010) found birds to be more sensitive to habitat quality than other variables, including fragment area, in urban fynbos fragments and their matrix types. Recent urban, agricultural and silvicultural development, along with the spread of invasive alien plants, has resulted in the fragmentation of sections of South Outeniqua Sandstone Fynbos (Filmalter & O'Keeffe, 1997; Russell et al., 2009, and see Chapter 1, Section 1). These habitat fragments are termed 'artificial fragments' in this study, owing to their anthropogenic origin, in order to differentiate them from the 'natural islands' which were isolated by environmental processes (Bond et al., 1988; Midgley & Bond, 1990, and see Chapter 1, Section 1).

The natural habitat islands are largely free from the confounding effects that are apparent in the artificial fragments, such as recent isolation age and the effects of the surrounding anthropogenically modified matrix (Ewers & Didham, 2006), and thus they provide a framework through which to determine biogeographic processes that may occur in the artificial fragments (Pickett & Thompson, 1978). A comparison of avifaunal response to the varying constraints of the natural islands and the artificial fragments may yield insights into the relative importance of individual fragmentation constraints in determining species response.

4.1.5 Post-fire vegetation age

Birds that use fynbos (known henceforth as fynbos-typical birds) are sensitive to the post-fire age of the vegetation in their habitat (Fraser, 1989; Martin & Mortimer, 1991; De Swardt, 1993; Geerts et al., 2012; Chalmandrier et al., 2013). Nectarivores in particular require mature, flowering plants from which to forage and are known to migrate locally in pursuit of this resource (Fraser, 1989, 1997; Cotton, 2007). Extensive fynbos areas are currently experiencing a generally shortened, unnatural fire-return interval (Kraaij et al., 2012a; Chalmandrier et al., 2013). Aside from the threat that this poses to the flora it also results in more young-growth vegetation and less usable habitat for fynbos-typical avifauna. This problem can become compounded considering that certain plant species are dependent on these birds for pollination (Bond, 1994; Pauw & Louw, 2012; Chalmandrier et al., 2013). Chalmandrier et al. (2013) suggested that a mosaic of different post-fire vegetation ages (see Forsyth & van Wilgen, 2008; Southey, 2009) should be maintained for the conservation of fynbos-typical avifauna. This can be achieved through prescribed burning of individual blocks of extensive fynbos in different years. Unfortunately fires of natural or accidental origin often burn vast tracts of land in large fynbos areas (Kraaij et al., 2012a; Chalmandrier et al., 2013) which makes the maintenance of a controlled mosaic difficult. Small fragments of fynbos burn less frequently than extensive areas (Pickett & Thompson, 1978; Bond et al., 1988, and see Chapter 3, Figure 3.1); because they are a smaller target for lightning strike and they are isolated from the spread of wildfire. Thus most are free from the problem of unplanned fires (although artificial fragments that are adjacent to areas of plantation forestry or that border on urban edges may get burnt more frequently (Kraaij & Vermeulen, 2010; Kraaij & van Wilgen, 2011)).

In this study I investigated the response of fynbos-typical bird communities to various aspects of artificially fragmented South Outeniqua Sandstone Fynbos. Specifically I investigated species-area relationships in the avifaunal community. I tested the existence of these relationships and compared them between three habitat configurations (natural habitat islands, artificial fragments and extensive ‘mainland areas’) and against the vegetation community. An avifaunal species-area relationship was expected to exist in isolated habitat configurations and that avifaunal communities in the artificial fragments would hold more extinction debt than vegetation communities due to the motility of birds and their associated metapopulation potential. Connectivity was examined in order to assess whether bird species can potentially migrate across matrix habitat in order to reach artificial fragments. Specifically I examined whether connectivity is associated with certain avifaunal migratory groups and with the nature of the surrounding matrix. I expected that connectivity would vary between avifaunal migratory groups and would be affected by the nature of the surrounding matrix. The pathways through which matrix-typical vegetation, capable of lowering bird habitat quality, enters artificial fragments were examined. I expected that these vegetation species are associated with the nature of the surrounding matrix and with frugivorous birds. Finally, I looked into the response of fynbos-typical avifauna to post-fire vegetation age, expecting nectarivores to be associated with vegetation that has a greater post-fire age, containing more mature, nectar yielding plants, than with recently burnt vegetation in which nectar sources are scarce. Through this the conservation potential of fynbos fragments has been highlighted, as stepping-stone habitats or resource refugia, in the conservation of fynbos avifauna.

4.2 MATERIALS AND METHODS

4.2.1 Study area

A detailed description and map of the study area can be seen in Chapter 1, (Section 1) and in Rebelo et al. (2006).

4.2.2 Site selection

A description of the various study sites that were used and an overview of the criteria involved in their selection can be seen in Chapter 3, (Section 2.2). The physical attributes of these sites are tabulated in Appendix 3.A and B.

4.2.3 Methods

The physical attributes of each site were calculated using Google Earth Pro on 2011 images in an elevation range of between 500 m and 1500 m. Isolation distance was calculated as the straight-line distance from the centre of the site to the perimeter of the nearest area of mainland fynbos. In the two cases where one fragment was sampled as two sites of different fire history, divided by a road, this distance was taken from the centre of the individual sites. In these cases, distance could also have been measured from the centre of the entire fragment, however the two methods yielded small differences (7% and 4%) and the decision was considered to be inconsequential. Percentage matrix edges were calculated for the three dominant matrix types in the study area; including forest, farm and plantation. Matrix heterogeneity was calculated as the number of discrete matrix types bordering on a particular fragment. All sample sites were assigned to a post-fire age group. Group one included fynbos that was burnt in the past ten years, group two between ten and twenty years ago, and group three over twenty years ago. Group three was left open-ended because the reliability of historical fire data starts to wane in records that are more than two decades old.

Two separate data sets were collected from each sample site, one concerning the vegetation community (see Chapter 3, Section 2.2) and the second concerning the avifaunal community. Functional trait abundances (see Appendixes 3.C and 4.A) were calculated from the inventory data using reference books (Courtenay-Latimer et al., 1967; Moriarty, 1982; Coates Palgrave, 1983; van Wyk & van Wyk, 1997; van Oudtshoorn, 1999; Goldblatt & Manning, 2000; Hockey et al., 2005; Manning, 2007).

Collection of vegetation data was based on the methods used by Bond et al. (1988), (see Chapter 3, Section 2.2). Similar methods were used to collect avifaunal data. Wandering transects were chosen over point counts for collection of avifaunal data in order to minimise the effects of differently aged vegetation with variable density (P. Hockey, personal communication, September 2011). The length of these transects varied with patch size and with vegetation density and was governed by bird species accumulation. When the discovery rate of bird species dropped to below two new species per hour, the sampling was considered complete. This point was reached within a single day for each plot. All avifauna data were collected between late September and early January, thus reducing any bias caused by bird's response to plant flowering time.

All bird species were recorded and identified on site where possible. A pair of 9 x 25 binoculars was used together with a field guide (Chittenden, 2007) in the field. Photographs were captured and audio recordings of calls were collected to aid in the *ex situ* identification of species.

Data were collected during spring and summer. Avifaunal transects were only conducted during the morning hours in daylight and at moderate temperatures. Sampling was not undertaken on days of moderate to strong winds, but did continue during light rain.

4.2.4 Statistical analysis

Inventories of species attributes and functional traits were compiled using data from both the vegetation and the avifaunal communities. Analyses concerned with fynbos-typical birds (known to use fynbos habitat to some degree) and matrix-typical birds (known to not use fynbos habitat) as classified by Hockey et al. (2005). Fynbos-typical and matrix-typical vegetation data were used in some analyses, where appropriate.

Bird and plant species-area regressions were conducted and compared between the three habitat configurations to assess the response of species to patch area and to investigate extinction debt in avifaunal communities, as done in Chapter 3, (Section 2.3). Regressions were calculated for subsets of the natural island and artificial fragment sites that were characterised by a common post-fire vegetation age. Similar comparisons were run between the vegetation and the avifaunal community regression curves of each habitat configuration. This was in order to see whether the avifaunal response to reduced area in the artificial fragments is comparable to that in the natural islands and in the mainland, and to the response of the vegetation community.

In order to investigate avifaunal connectivity, the distributions of certain bird functional trait groups between the three habitat configurations were tested using modified Chi-square tests as used by Bond et al. (1988) and in Chapter 3, (Section 2.3). This was also done between the habitat configurations under more or less isolation distance and matrix heterogeneity. Two isolation distance classes (shortest distance to mainland fynbos) were used: ‘proximate patches’ included those that are isolated by less than 2000 m and ‘distant patches’ are isolated by over 2000 m. Habitat heterogeneity was measured as the number of discrete matrix types that form an edge directly with the artificial fragment in question. In these tests, the mainland data were used to calculate the expected value in the natural islands and the artificial fragments (this value was calculated from the natural island data in comparisons between the natural islands and the artificial fragments). This calculation involved the scaling of the frequencies of each functional trait group to the artificial fragment or natural island species total. These tests adopt the null hypothesis that the frequencies in each functional trait group do not differ between the observed and the expected value. The technical details of these analyses can be seen in Chapter 3, Section 2.3. Functional groups that were tested included feeding guilds and migratory groups (see Hockey et al., 2005; Appendix 4.A). Only fynbos-typical bird species were included in these analyses.

To assess the response of species groups to the environmental variables associated with habitat fragmentation and altered fire return intervals, canonical correspondence analyses were run using the statistical package CANOCO 4.5 for Windows (Ter Braak, 1986; Ter Braak & Šmilauer, 2002). Data used in the first analysis were concerned with all bird species observed, ranked according to their known nectar usage, and those used in the second analysis were concerned with matrix-typical vegetation species. These vegetation species were sorted into three groups, namely: species typical of agricultural lands (typically herbs and graminoids), species typical of silviculture or that are known as invasive alien plants (typically alien shrubs or trees), and forest-typical species. Data were not transformed and the biplot scaling was focused on the inter-species distances. Only data concerning the artificial fragments were used in the ordinations because the mainland data were not suitable for

use in canonical correspondence analyses, and the natural island data did not represent the full amount of variation with respect to post-fire age that is useful in these analyses.

4.3 RESULTS

4.3.1 Species-area relationships

The species-area regressions that result from the vegetation and the avifaunal data in all three habitat configurations are presented in Figure 4.1. Both avifaunal and vegetation species richness increase significantly ($p < 0.05$) with sample area in both the natural islands and in the mainland plots, however no such relationships are observed in the artificial fragments despite a greater sample size (Figure 4.1;Table 4.1).

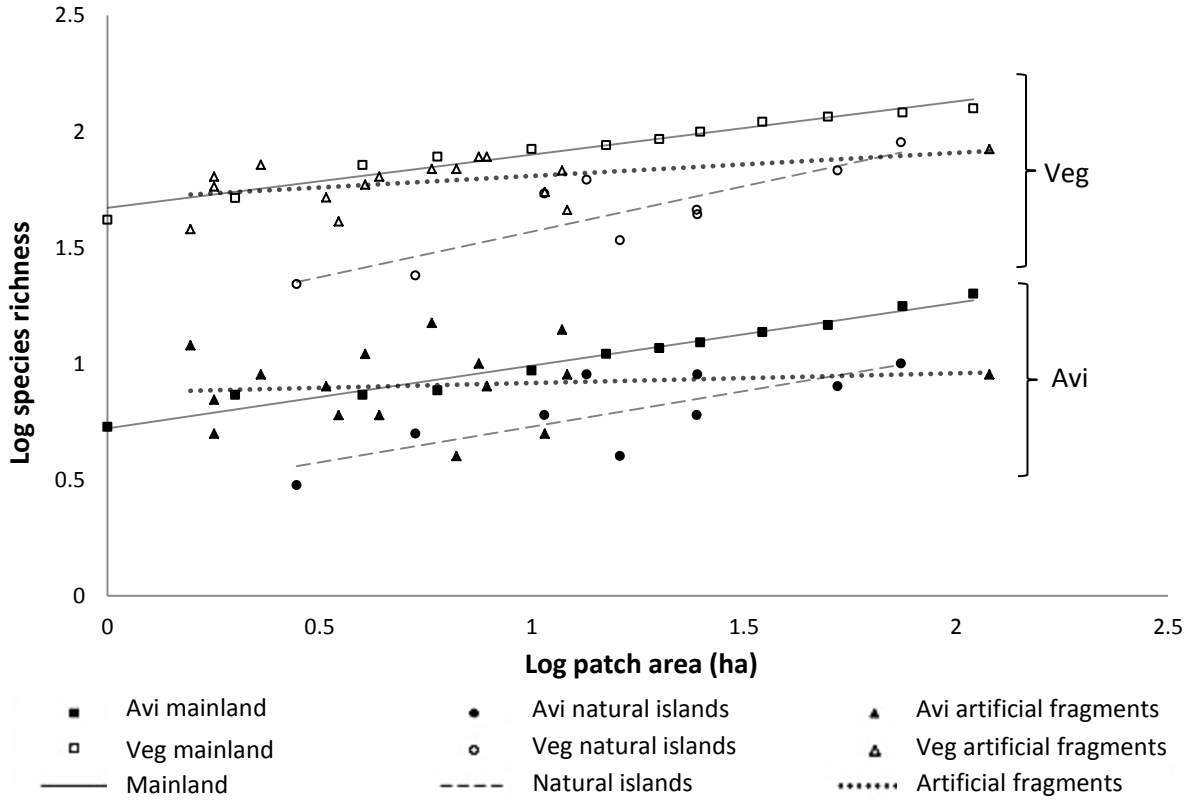

Figure 4.1 – Species-Area Plot. AVI= Avifauna, VEG= Vegetation. Vegetation data included fynbos and forest margin species only. AVI data included bird species identified by Hockey et al. (2005) as using fynbos to some degree, as opposed to those not found to use fynbos. Mainlands (both AVI & VEG) are represented by a logged average of the three accumulation series. Regression lines: Solid= mainland; Dotted= natural islands; Dashed= artificial fragments. The vegetation component of the plot is adapted from Chapter 3, Figure 3.4.

The slopes of the avifaunal species-area curve for each of the three habitat configurations do not differ significantly from those of the vegetation community (Figure 4.1; Table 4.2) although the avifaunal species-area curves (for each of the three habitat configurations) have lower Y-intercepts (Figure 4.1); this can be attributed to the relative size of the two species pools. A total of 488 plant species were observed in the study compared to 87 bird species, of which 370 and 45 respectively were classified as fynbos-typical.

Table 4.1 – Species-area regression of fynbos typical species (logged) in each of the three fynbos habitat configurations. "AVI" = bird species, "VEG" = plant species. The three habitat configurations include Natural Islands (NI), Artificial Fragments (AF) & Mainland (ML). The vegetation component of the table is adapted from Chapter 3.

	Data	Regression coefficient	1 SE	*t*-value	*P*-value	R^2
i)	NI-AVI (log)	0.307	0.0940	3.261	0.0139	0.603
ii)	NI-VEG (log)	0.392	0.0869	4.512	0.00276	0.744
iii)	AF-AVI (log)	0.0417	0.0951	0.439	0.668	0.0136
iv)	AF-VEG (log)	0.0997	0.0516	1.931	0.07397	0.210
v)	ML-AVI (log)	0.270	0.0139	19.407	<0.0001	0.974
vi)	ML-VEG (log)	0.229	0.0152	15.054	<0.0001	0.958

The vegetation in the artificial fragments was found to be going through extinction debt (see Chapter 3, Section 4). The species-area curves for artificial fragments lie between the mainland and the natural island curves (Figure 4.1) and there is a significant difference in the regression slopes between the artificial fragments and the two natural fynbos configurations (Table 4.2). Avifaunal data are more variable than vegetation data from the same artificial fragments, with some plots locating above the mainland curve (Figure 4.1). There is also a significant difference between the resulting avifaunal species-area curve and that of the mainland, which has a steeper gradient, although not significantly different to that of the natural islands.

Table 4.2 – Regression Slope Comparisons. NI= Natural Island; AF= Artificial Fragment; ML= Mainland. Suffix: "v"= Floral Richness, "a" = Avifaunal Richness. Significant values indicate a difference between two regression curves.

	Test	1 SE	DF	*t*-value	*P*-value
i)	NIv/NIa	0.128	14	0.667	0.515
ii)	NIv/AFv	0.0952	21	3.069	0.00582
iii)	NIa/AFa	0.150	21	1.772	0.0910
iv)	AFv/AFa	0.108	22	0.536	0.598
v)	AFv/MLv	0.0538	16	2.398	0.0291
vi)	AFa/MLa	0.0961	15	2.373	0.0325
vii)	MLa/MLv	0.0206	20	1.997	0.0597

4.3.2. Connectivity and matrix effects

Relative to the total avifaunal species richness of each configuration, the artificial fragments have a higher percentage than the mainland in all feeding guilds except for insectivores and nectarivores (Figure 4.2). The natural islands have the lowest percentage of generalists (11 %) and granivores (8 %), but they also have the highest percentage of frugivores (11 %). The mainland has a lower percentage of frugivores (4 %) and carnivores (6 %) than the two isolated configurations.

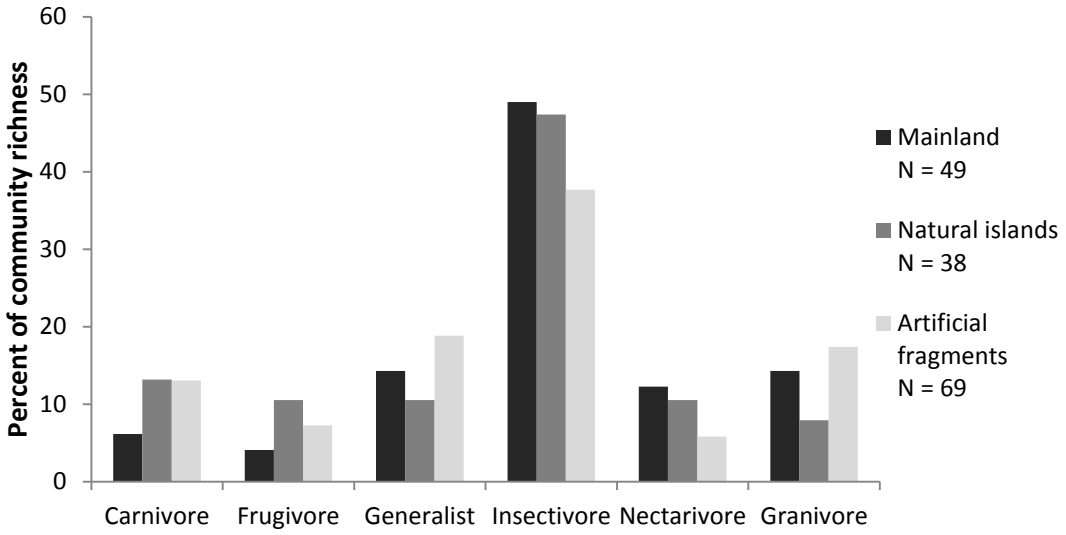

Figure 4.2 – The percentage contribution of each bird feeding guild to the total species richness of the three fynbos configurations: mainland natural islands and artificial fragments. Data include total species counts for which *N*-values are provided.

The frequencies of migratory avifaunal groups do not differ significantly between the three fynbos configurations when analysed with modified chi-squared tests using fynbos-typical bird data. This holds true for data concerning all habitat patches, data concerning only the less isolated patches, and for data concerning only the more isolated patches within each configuration.

Table 4.3 – Results from modified Chi-squared tests of avifaunal feeding guild distributions (FG) between the different habitat configurations. ML= Mainland, NI= Natural Islands, AF=Artificial Fragments. In the first five tests, mainland data were used to calculate the expected value. In the last two tests, natural island data were used to calculate the expected value. "Proximate" refers to patches that are isolated by less than 1000 m; "Distant" refers to patches isolated by more than 1000m; "All" refers to all of the patches in one particular habitat configuration. χ^2 is Chi-square; NS= P >0.05; *=P <0.05. The last two columns show which feeding guilds are overrepresented (Increase) and which are underrepresented (Decrease) in the observed data. Feeding guilds are presented in Appendix 4.A.

	Trait	Configuration	Group	*p*-value	χ^2-value	Increase	Decrease
i)	FG	ML v AF	All	NS	12.37	-	-
ii)	FG	ML v NI	All	*	15.71	Frugivore	Granivore
iii)	FG	ML v NI	Proximate	*	16.58	Frugivore	Predator
iv)	FG	ML v AF	Distant	NS	12.37	-	-
v)	FG	ML v NI	Distant	NS	3.97	-	-
vi)	FG	NI v AF	All	NS	4.65	-	-
vii)	FG	NI v AF	Distant	*	1.75	Granivore	Nectarivore

Frugivores are overrepresented on natural islands relative to the mainland, irrespective of their isolation distance (Table 4.3). Granivores and predators are underrepresented in the natural islands and in the proximate natural islands respectively. The frequencies in the distant natural islands and in all of the artificial fragment combinations do not differ significantly from those in the mainland.

The feeding guild frequencies between the natural islands and the artificial fragments are not significantly different. However, frequencies do differ significantly in plots that are distant from the mainland, and granivores are overrepresented while nectarivores are underrepresented in the distant artificial fragments relative to the distant natural islands. The Cape Sugarbird (*Promerops cafer*) is an important fynbos nectarivore that is present in the mainland areas but absent from both the artificial fragments and the natural islands (Appendix 4.A).

Modified chi-squared tests concerned with the distribution of feeding guild and migratory group frequencies – using data grouped according to the level of heterogeneity in the surrounding matrix – do not yield significant differences.

4.3.3 Post-fire vegetation age

The response, shown as species-environmental variable associations, of both fynbos-typical and matrix-typical bird species to vegetation post fire age in the artificial fragments, is illustrated by the CCA ordination (Ter Braak, 1986; Ter Braak & Šmilauer, 2002), (Figure 4.3). The environmental variables of isolation distance and percentage edge composition are also included.

The majority of the bird species in the artificial fragments are associated with an environmental axis that is formed by the covariables post-fire age category one and plantation edge, together with the associated variable of forest edge percentage. Together these are negatively related to the covariables: isolation distance and farmland edge percentage. Species richness is not explained by any particular component of this axis but the axis does represent a gradient of nectarivore richness. All four of the obligate nectarivores and most of the facultative nectarivores are positively associated with fynbos vegetation that has burnt within the past ten years and with high forest edge percentages. These nectarivores are also negatively associated with high farmland edge percentages.

A second environmental axis is formed by the variables of post-fire vegetation age two and three – vegetation that was last burnt between ten and twenty years ago and that which was last burnt over twenty years ago respectively. There is a strong association between a large group of bird species and this gradient: the majority of the species are associated with vegetation age three. There is a weak presence of nectarivores in this group.

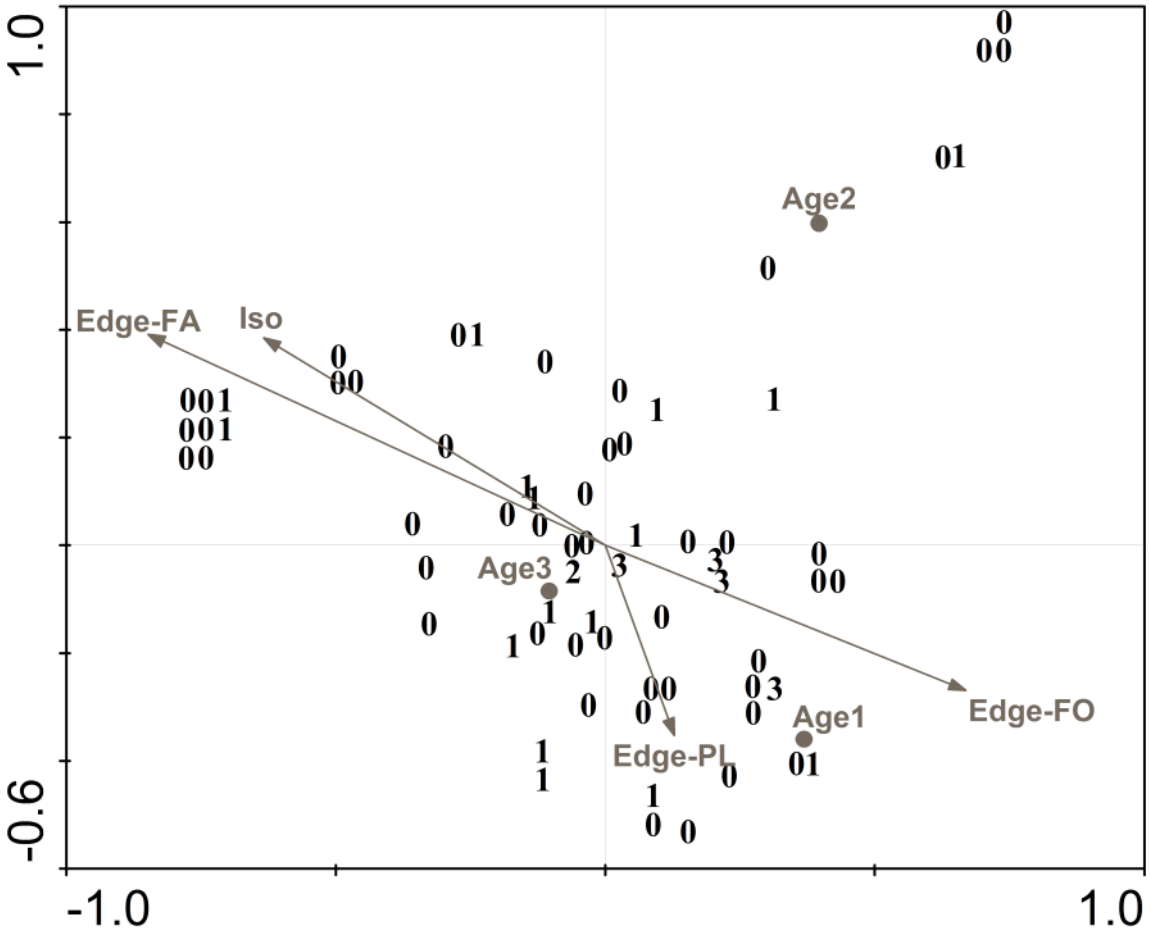

Figure 4.3 – CCA ordination indicating the response of all bird species observed within the artificial fragments to post-fire vegetation regrowth, sample isolation and edge composition. Eigenvalues: 0.424 (axis 1) and 0.356 (axis 2); cumulative percentage variance of species data: 10.3 (axis 1) and 18.9 (axis 2) and of species-environment relation: 25.2 (axis 1) and 46.4 (axis 2). Numbers 0 – 3 refer to the importance of nectar in each bird species diet according to Hockey et al. (2005) with "0" representing non-nectarivores, "1" representing facultative nectarivores known to feed on nectar occasionally, "2" representing facultative nectarivores for which nectar is a secondary food, and "3" indicating obligate nectarivores. Edge-FO- percentage of edge with forest; Edge-FA- percentage of edge with farmland; Edge-PL- percentage of edge with plantation; Iso- isolation distance (m); Age1- burned within previous 10-years; Age2- burned between 10 and 20 years ago; Age3- burned more than 20 years ago.

In the absence of confounding fragmentation effects, mainland avifauna clearly responded to post-fire vegetation age. There were proportionally more generalist and granivore bird species in mainland fynbos that has been burned within the past ten years than in fynbos that is over twenty years old (Figure 4.4). Nectarivores show an inverse trend. Nectarivore species in the older growth fynbos are relatively more abundant than in the recently burned areas. This positive association between nectarivore richness and post-fire vegetation age is the inverse of what is seen in the artificial fragments (Figure 4.3).

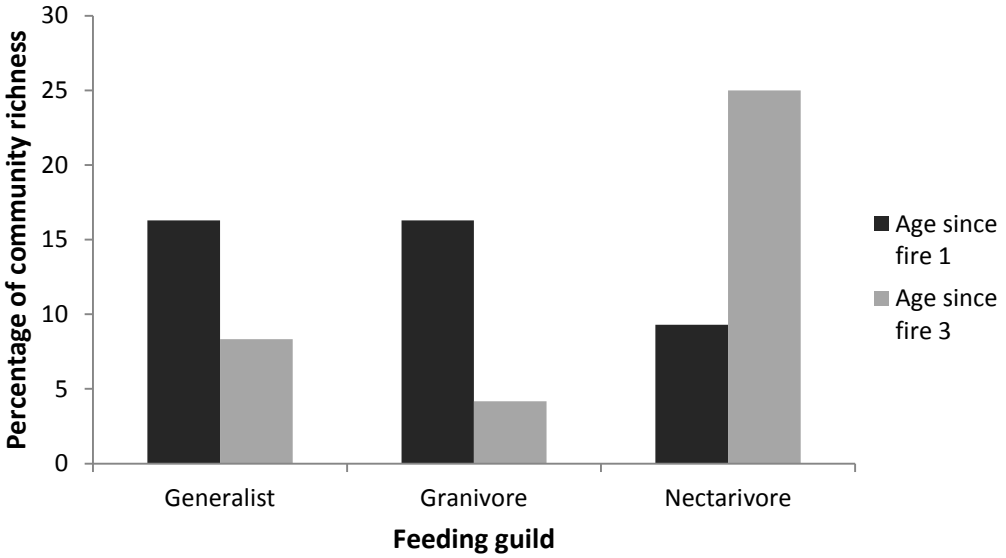

Figure 4.4 – The response of three bird feeding guilds to post fire age in the mainland plots shown with percentage of community richness data. Only post fire age 1 (N=26) and 3 (N=10) are included since there were no post fire age 2 sites in the mainland areas.

4.3.4 Habitat quality and the matrix

The results of a CCA illustrate the association of matrix-typical vegetation species in the artificial fragments with environmental variables associated with the fragments and with the surrounding matrix (Figure 4.5). In general, this analysis shows a relationship between the nature of the matrix types that border the artificial fragments and the type of non-native species that enter the fragments. The role of frugivores in dispersing particular plant species into the fragments is also highlighted through this analysis.

Each one of the three groups of matrix-typical vegetation species (cosmopolitan weeds, herbs and graminoids; alien shrubs and trees; forest-typical vegetation species) is associated with a particular set of covariables which form three distinct axes. One environmental variable in each of these sets of covariables describes the percentage of the fragment edge that is shared with a particular matrix type. Specifically there is an association between alien shrubs and trees and the covariables of plantation edge percentage and matrix heterogeneity 2 (fragments that are bordered by two distinct matrix types). Cosmopolitan weeds, herbs and crop or pasture graminoids are associated with the covariables of farmland edge percentage and matrix heterogeneity 3 (fragments that are bordered by three distinct matrix types). Forest-typical plant species are associated with the covariables of forest edge percentage and fragment area. A unique group of forest-typical plants and cosmopolitan weeds, herbs and crop or pasture graminoids is associated with frugivorous bird richness.

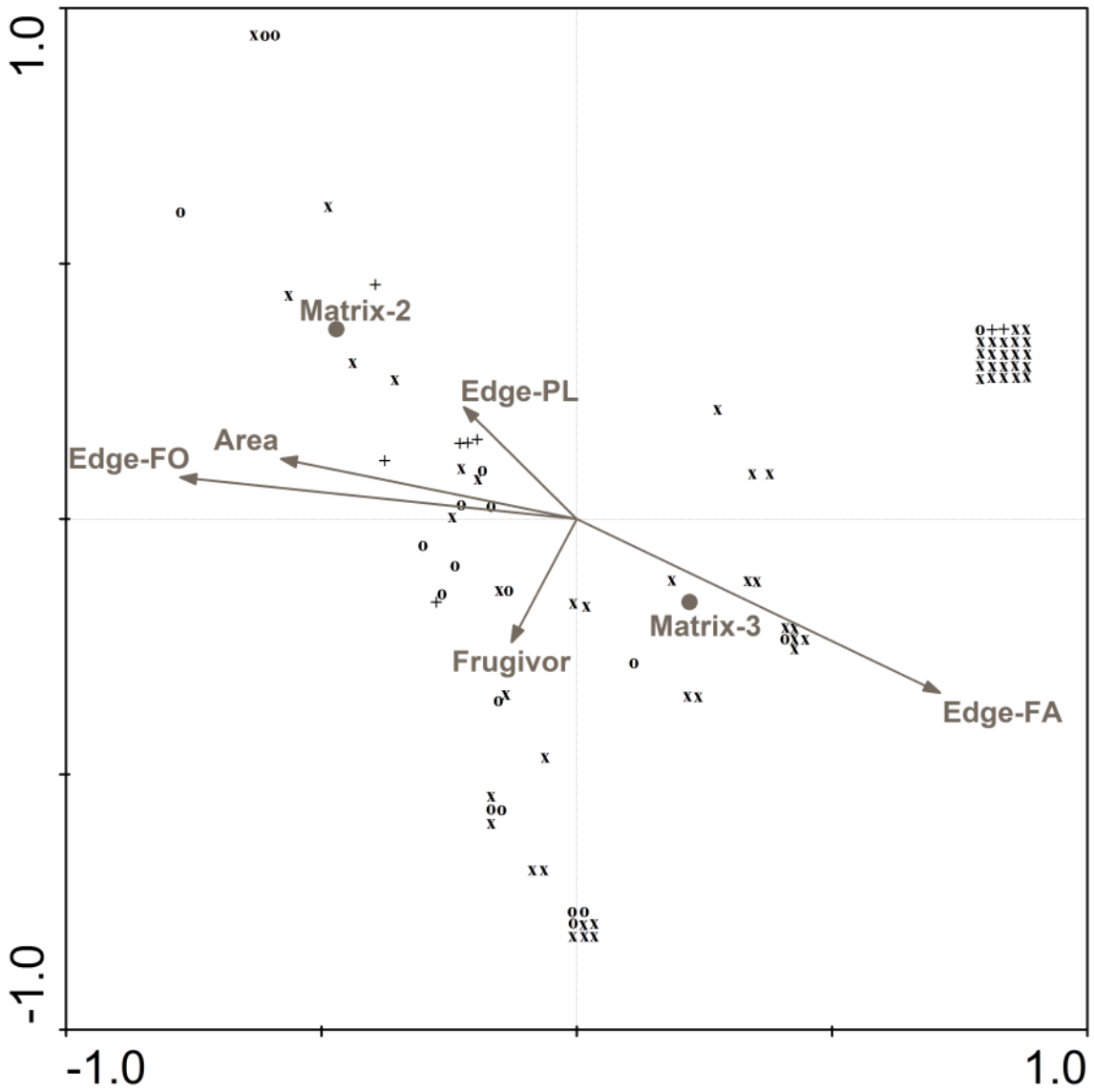

Figure 4.5 – CCA ordination indicating the response of matrix-typical vegetation species within the artificial fragments to the environmental variables associated with matrix type and edge composition. Eigenvalues: 0.603 (axis 1) and 0.395 (axis 2); cumulative percentage variance of species data: 21.8 (axis 1) and 36.1 (axis 2) and of species-environment relation: 30.7 (axis 1) and 50.9 (axis 2). "X" represents vegetation species typical of agricultural lands (typically herbs and graminoids); "+" represents alien shrubs and trees that are typical of plantation forestry or that are known as invasive alien plants; "O" represents forest-typical vegetation species. Edge-FO- percentage of edge with forest; Edge-FA- percentage of edge with farmland; Edge-PL- percentage of edge with plantation; Matrix-2- bordered by two matrix types; Matrix-3- bordered by three matrix types; Area- sample area (ha); Frugivor- frugivore species richness.

4.4 DISCUSSION

I investigated the response of avifauna to the fragmentation of South Outeniqua Sandstone Fynbos habitat and found that birds display slightly more resilience to certain fragmentation effects than initially predicted. The response of birds to reduced patch area showed significant species-area relationships in the natural islands, similar to that observed in the vegetation community. Birds in the artificial fragments respond to area-independent factors such as vegetation and habitat quality or the nature of the surrounding matrix.

I then tested the response of different avifaunal migratory groups and feeding guilds to various levels of isolation and matrix composition in order to assess connectivity in the fragments. Migratory groups are not affected by isolation distance, and their frequencies remain the same throughout the three habitat configurations. Feeding guilds do vary between habitat configurations under certain conditions, but nectarivores – which are important pollinators of fynbos plants (Rebelo & Siegfried, 1985; Rebelo, 1987; Johnson, 1992; le Maitre & Midgley, 1992) – do not respond to isolation distance. Nectarivores are more associated with certain matrix types than others. I investigated the response of avifauna to post-fire vegetation age and found that this differs between bird feeding guilds. Nectarivore response varies between the artificial fragments and the mainland areas. Lastly I looked into the presence of matrix-typical vegetation in the artificial fragments and found that these species are associated with the surrounding matrix and with frugivore richness. Matrix-typical vegetation can potentially reduce the quality of avifaunal habitats. These results suggest that artificial fragments of South Outeniqua Sandstone Fynbos may have value as resource refugia and 'stepping-stone' reserves for avifauna under the pressures of habitat fragmentation and changing fire regimes.

4.4.1 Species-area considerations

The positive bird species-area relationship in the natural islands is typical of isolated biotic communities as is the weak bird species-area relationship in the mainland fynbos (Dengler, 2009; Kuussaari et al., 2009). The slope of the avifaunal species-area response curve did not differ from that of the vegetation community in any of the three habitat configurations; only the y-intercept did. This indicates that biological communities that differ in the size of their species source pools and their motility (birds can migrate to and from a fragment more easily than plants) can share a similar response to reduced fragment area. These patterns are somewhat contrary to my predictions. Communities that are going through ecological relaxation are typically positioned between the mainland species-area curve and a new quasi equilibrium species-area curve in a species-area plot (Chorley & Kennedy, 1971; Malanson, 2008; Kuussaari et al., 2009; Hylander & Ehrlén, 2013). Since avifauna are relatively short-lived and are more motile that vegetation species, one would expect slower ecological relaxation to occur in the artificial fragment avifauna, as suggested by Tilman (1994). My results showed that the species richness of birds in the artificial fragments does not represent a stable species-area relationship, but – in many of the fragments – it exceeds that even of the mainland fynbos. Although it is likely that these birds are under area-based extinction debt (and respond primarily to the effect of area on vegetation richness), the elevated bird richness in the artificial fragments could be attributed to favourable conditions that are temporarily provided by the surrounding matrix. If more resources or niches become available in fragmented habitat than in continuous habitat and if these fragments are able to support elevated bird species richness then, with time, colonist species will arrive. Thus, through this non area-based 'immigration credit' (Hanski, 2000; Jackson & Sax, 2009), the area-based extinction debt is cancelled out. Of course, these improved bird habitat conditions that I propose in the artificial fragments may, if even existent, be temporary and change as negative fragmentation effects increase. These bird communities will also

likely experience further area-based extinctions in the future as the debt that exists in the vegetation community is 'paid' off (see Chapter 3, Section 4.).

Community responses in which area is of secondary importance have been observed in other studies of fragment avifauna in fynbos (Kieck, 2009) and other ecosystems (Dean & Bond, 1994). Lees and Peres (2006) found that habitat quality and fragment geometry better explain the bird species richness of tropical forest fragments than the physical area of the fragment. They also found that fragment geometry can influence the pattern of fragment bird species-area relationships.

4.4.2. Connectivity

The fynbos-typical bird migratory group frequencies in the natural islands indicate that avifaunal connectivity is not limited by isolation distance. The natural islands are not subject to the same potentially confounding factors that artificial fragments are, such as the effects of a diverse surrounding matrix and a relatively young isolation age. It can therefore be inferred that avifauna in the artificial fragments will be similarly unconstrained by isolation distance. Connectivity is not significantly reduced by the nature of the surrounding matrix because the migratory group frequencies in the artificial fragments are not influenced by the number of matrix types that surround a fragment. These frequencies also remained constant in the artificial fragments – surrounded by heterogeneous matrix – relative to the mainland and the natural island frequencies. Local migrant species are present in the artificial fragments in proportionally similar numbers to those in the mainland, which suggests that avifaunal groups that are known to migrate naturally will continue to migrate to or from artificial fragments.

My investigation into the feeding guild frequencies of the fynbos patches did detect some deviation in the natural islands relative to the mainland, and between the natural islands and the artificial fragments at large isolation distances. Importantly nectarivore richness is underrepresented in the distant artificial fragments relative to the distant natural islands. However the feeding guild frequencies in the artificial fragments, nectarivores included, remained consistent with those in the mainland sites throughout. This suggests that fynbos-typical nectarivores are capable of local migration across a Southern-Afrotemperate Forest (Mucina & Geldenhuys, 2006) matrix, or across human modified matrix. It is apparent from my results that nectarivores show preference to artificial fragments that are surrounded to a large degree by indigenous forest or timber plantations than those that are bordered by farmland. Nectarivores are important pollinators of fynbos vegetation (Rebelo & Siegfried, 1985; Rebelo, 1987; Johnson, 1992; le Maitre & Midgley, 1992). Previous studies have found nectarivores to migrate locally while tracking availability of their nectar resource (Johnson, 1992; Fraser, 1997; Cotton, 2007). Fynbos-typical nectarivores often have to undergo altitudinal migration in search of nectar yielding flowers which become seasonally available at different altitudes (Siegfried, 1983; Rebelo, 1987; Johnson, 1992). The absence of the Cape Sugarbird (*Promerops cafer*) from all of the natural islands and artificial fragments must be noted because this endemic species is an important pollinator of various Proteaceae species (Martin & Mortimer, 1991; Fraser, 1997; Collins & Rebelo, 2006; Geerts et al., 2012; Lee & Barnard, 2012). Sugarbirds feed exclusively on nectar from Proteaceae flowers and on the invertebrates that are associated with these flowers (Skead, 1967; Mostert et al., 1980; Calf et al., 2003; Hockey et al., 2005). These plants were in flower during sampling. Small, isolated fynbos patches may not have the species richness of Proteaceae or the abundance of Proteaceae plants that are required by Cape Sugarbirds. Alternately, Sugarbird movements could be restricted by the nature of the surrounding matrix to a greater degree than other nectarivores. Sugarbirds are known to fly large distances (the furthest recorded migration being 365 km), however they seldom leave fynbos habitat (Fraser, 1997; Calf et al., 2003; Hockey et al., 2005).

In general, frugivores are overrepresented in the natural islands. This is attributed to the inclusion of many frugivore species, such as the African Olive-Pigeon (*Columba arquatrix*) and Knysna Turaco (*Tauraco corythaix*), from the indigenous forest (Phillips, 1927; Manders & Richardson, 1992) that surrounds the natural islands and constitutes a large proportion of the average fragment boundary. The significant overrepresentation of granivores in the artificial fragments relative to the natural islands is attributed to the presence of graminoid vegetation species in the surrounding matrix and in some of the fragments. Agricultural land with crops and pastures typically has a higher abundance of graminoids than the indigenous forest matrix which surrounds the natural islands. Literature suggests that granivores in habitat fragments that are surrounded by agriculture are able to use the matrix and feed on cereal crops and graminoids to some degree (Wilson et al., 1999; Mangnall & Crowe, 2003). It is likely that this applies to granivores in fragments of South Outeniqua Sandstone Fynbos as well. The granivore frequency in the artificial fragments does not differ to that in the mainland, and thus is not a concern.

I suggest that future research should address the question of bird species connectivity with empirical evidence of bird migration at the species level. This may yield greater insights into the distribution of ecologically important species such as the Cape Sugarbird. Inferences drawn from the presence or absence of specific migratory groups under various levels of isolation and matrix type do however address my questions concerning community dynamics.

4.4.3 Post-fire age

I found that nectarivore response to post-fire vegetation age contrasts between mainland fynbos and artificial fragments. My results show that nectarivore presence more than doubles in old growth mainland fynbos that has remained fire free for at least twenty years than in recently burnt fynbos sites. This is consistent with other studies that have documented increased fynbos-typical nectarivore abundance with post-fire vegetation age (e.g. Chalmandrier et al., 2013). Paradoxically, the opposite trend was observed in the artificial fragments where nectarivores are more associated with younger post-fire vegetation than with older vegetation. I suspect that these apparently contrasting responses could be more due to the selection of age categories in this study than to the biological preference of nectarivores. Post-fire age category three is open ended. It can potentially contain mature vegetation nearing the upper limit of its natural fire-return interval (twenty-six years, Kraaij et al., 2012a, 2013b) yet still able to provide nectar, and it can include senescent vegetation that has not burned for many decades. Many of the mainland sites fall into this category, but because I did not observe very old, senescent vegetation in them I can assume from my observations that these sites fall into the former portion of this final age category. Artificial fragments that fell into age category three appeared to be much further into this category because I frequently observed senescent vegetation therein, and because these area-constrained habitats receive fire less frequently than the mainland (Pickett & Thompson, 1978; Bond et al., 1988, and see Chapter 3, Section 3.1). Although fragment vegetation in age category one has had less time to reach maturity, its post-fire age most likely lies just above the minimum fire return interval of eight years (Kraaij et al., 2012a, 2013) meaning that it already has the potential to provide nectar to nectarivores. Many fynbos geophytes and species of the genus *Erica* flower and produce nectar shortly after a fire (Rebelo et al., 1984; le Maitre & Midgley, 1992; Lamont & Downes, 2011; Chalmandrier et al., 2013). Consequently I consider the result drawn from the mainland sites to be a more appropriate answer to the question of nectarivore response to post-fire age.

Chalmandrier et al. (2013) found that most of the plant functional changes common in post-fire vegetation occur within six years of a fire. I speculate that nectarivores may use South Outeniqua

Sandstone Fynbos vegetation that has burnt within the last ten years, provided that it is at least six years old. It is also possible that this age category of young post-fire vegetation can become a greater resource to fynbos nectarivores when habitat fragments become smaller and more isolated (Brotons et al., 2003). These suggestions are supported by my findings of bird response to post-fire vegetation age in the artificial fragments, as discussed previously. This has important conservation implications for fynbos-typical nectarivores considering that there is a documented reduction of recent fire return intervals in extensive fynbos areas throughout the Cape Floristic Region (Forsyth & van Wilgen, 2008; Southey, 2009; Kraaij et al., 2012a, 2012b) as highlighted by Chalmandrier et al. (2013). Additional to post-fire vegetation age, it is also likely that changes in the other two components of the fire regime – burn intensity and burn season – will promote vegetation diversity and thus high quality bird habitat (Thuiller et al., 2007). The constraint of one or more of these fire regime components by aspects of the artificial fragments could result in reduced habitat quality. Mainland fynbos in age category one also contained twice or more the percentage of generalist and granivore species than age category three. This trend is typical of recently burnt fynbos habitats (Chalmandrier et al., 2013).

4.4.4 Habitat quality

Birds are sensitive to the quality of their habitat (Parker et al., 2005; Briggs et al., 2007; Kieck, 2009) which is often linked to the quality of the vegetation component of their habitat, as seen in Section 4.3 of this chapter. I found that introduced matrix-typical plants, capable of changing the quality of vegetation habitats, are associated with the particular matrix type that dominates the fragment-matrix boundary, and that forest-typical vegetation species and certain cosmopolitan weeds are also associated with frugivorous bird species richness. Frugivores, which are overrepresented in the natural islands, are known to disperse ornithochorous forest tree species and certain invasive alien plants into fynbos habitats (Phillips, 1927; Manders & Richardson, 1992). Artificial fragments already contain 42 % more matrix-typical vegetation species than the natural islands (Chapter 3; Figure 3.5). Although these introductions do not reflect vegetation community shift or reduced bird habitat quality, such consequences could ultimately occur (Buckley et al., 2006). Introduced invasive alien plants can potentially alter the fire regime within a fynbos habitat and compete aggressively with local vegetation (see Chapter 5, Section 2.2).

4.4.5 Implications

The response of avifauna to the various aspects of habitat fragmentation has implications for the persistence of bird communities and for the ecological mutualisms in which they are engaged, particularly in areas that have suffered from severe habitat loss and fragmentation. An understanding of this response provides an indication of the extent to which avifauna is threatened by fragmentation and direction to conservation agencies regarding the protection of avifauna and the selection of areas for its conservation. The results of this study show that avifauna, typical of the South Outeniqua Sandstone Fynbos, is not particularly sensitive to the fragment constraints of isolation distance or the nature of the surrounding matrix, specifically with regard to inter-patch migration. Thus the artificial fragments of South Outeniqua Sandstone Fynbos represent areas of potential habitat for avifaunal communities. These bird communities do show sensitivity to post-fire vegetation age and fragment area, though it is suspected that this apparent response to patch area is in fact a mirror response to the vegetation species-area relationship of the patch. This relationship is ultimately determined by the unique fire-return interval of each patch. The prescription of a calculated and controlled fire regime may be of primary importance in the conservation of fynbos fragments for avifauna and the vegetation that they use.

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Appendix 4.A – List of avifauna species and functional groups recorded in this study. All data regarding species biology were from Hockey et al. (2005). Feeding guilds (FG) are abbreviated as follows: CA – carnivore (excludes insectivores); FR – frugivore; GN – generalist; GR – granivore; IN – insectivore; NE – nectarivore. Nectar usage is ranked from 0 to 3 and is interpreted as follows: 0 – no usage of nectar; 1 – occasional nectar usage; 2 – nectar usage as secondary food; 3 – obligate nectarivore. Fynbos usage was recorded as: "SU" (some usage) – species is known to use fynbos habitat in some way; "NU" (no usage) – species is not known to use fynbos habitat. Migratory groups are interpreted as follows: AM – altitudinal migrant; IA – intra-African migrant; NO – nomad; RE – resident; SL – some local movement. Note that some species are characterised by more than one group.

Common name	Family	Scientific name	F G	Nectar usage	Fynbos usage	Migratory group
African Goshawk	ACCIPITRIDAE	*Accipiter tachiro*	CA	0	NU	RE
Egyptian Goose	ANATIDAE	*Alopochen aegyptiaca*	GN	0	SU	NO/RE
Sombre Greenbul	PYCNONOTIDAE	*Andropadus importunus*	FR	1	SU	RE
Orange-breasted Sunbird	NECTARINIIDAE	*Anthobaphes violacea*	NE	3	SU	RE
Bar-throated Apalis	CISTICOLIDAE	*Apalis thoracica*	IN	0	SU	RE
Lemon Dove	COLUMBIDAE	*Aplopelia larvata*	GR	0	NU	RE
Little Swift	APODIDAE	*Apus affinis*	IN	0	SU	IA/RE
African Black Swift	APODIDAE	*Apus barbatus*	IN	0	SU	IA/RE
White-rumped Swift	APODIDAE	*Apus caffer*	IN	0	SU	IA
Cape Batis	MALACONOTIDAE	*Batis capensis*	IN	0	NU	RE/SL
Hadeda Ibis	THRESKIORNITHIDAE	*Bostrychia hagedash*	IN	0	SU	NO/RE
Little Rush-Warbler	SYLVIIDAE	*Bradypterus baboecala*	IN	0	NU	RE/SL
Jackal Buzzard	ACCIPITRIDAE	*Buteo rufofuscus*	CA	0	SU	RE/SL
Forest Buzzard	ACCIPITRIDAE	*Buteo trizonatus*	CA	0	SU	RE/SL
Red-capped Lark	ALAUDIDAE	*Calandrella cinerea*	GR	0	NU	NO/RE/SL
Green-backed Camaroptera	CISTICOLIDAE	*Camaroptera brachyura*	IN	0	NU	RE/SL
Greater Striped Swallow	HIRUNDINIDAE	*Cecropis cucullata*	IN	0	SU	IA
Familiar Chat	MUSCICAPIDAE	*Cercomela familiaris*	IN	0	NU	RE/SL
Amethyst Sunbird	NECTARINIIDAE	*Chalcomitra amethystina*	NE	3	NU	NO/RE/SL
Olive Bush-Shrike	MALACONOTIDAE	*Chlorophoneus olivaceus*	IN	0	NU	AM/RE
Klaass Cuckoo	CUCULIDAE	*Chrysococcyx klaas*	IN	1	NU	IA/RE
Greater Double-collared Sunbird	NECTARINIIDAE	*Cinnyris afer*	NE	3	SU	RE/SL
Southern Double-collared Sunbird	NECTARINIIDAE	*Cinnyris chalybeus*	NE	3	SU	RE/SL
Lazy Cisticola	CISTICOLIDAE	*Cisticola aberrans*	IN	0	NU	RE/SL
Neddicky	CISTICOLIDAE	*Cisticola fulvicapilla*	IN	1	SU	RE
Wailing Cisticola	CISTICOLIDAE	*Cisticola lais*	IN	0	SU	RE
Grey-backed Cisticola	CISTICOLIDAE	*Cisticola subruficapilla*	IN	0	SU	RE/SL
Cloud Cisticola	CISTICOLIDAE	*Cisticola textrix*	IN	0	SU	RE
Levaillants Cisticola	CISTICOLIDAE	*Cisticola tinniens*	IN	0	NU	RE
White-backed Mousebird	COLLIDAE	*Colius colius*	FR	1	NU	RE/SL
Speckled Mousebird	COLLIDAE	*Colius striatus*	FR	1	NU	AM/RE/SL
African Olive-Pigeon	COLUMBIDAE	*Columba arquatrix*	FR	0	NU	RE/SL
Grey Cuckooshrike	CAMPEPHAGIDAE	*Coracina caesia*	IN	0	NU	RE/SL
White-necked Raven	CORVIDAE	*Corvus albicollis*	CA	0	NU	RE
Cape Crow	CORVIDAE	*Corvus capensis*	CA	0	SU	RE
Cape Robin-Chat	MUSCICAPIDAE	*Cossypha caffra*	IN	0	SU	AM/RE
Chorister Robin-Chat	MUSCICAPIDAE	*Cossypha dichroa*	IN	0	NU	AM/RE

Common Quail	PHASIANIDAE	*Coturnix coturnix*	GN	0	SU	AM
Yellow Canary	FRINGILLIDAE	*Crithagra flaviventris*	GR	1	SU	NO/RE/SL
Forest Canary	FRINGILLIDAE	*Crithagra scotops*	GR	0	SU	RE
Brimstone Canary	FRINGILLIDAE	*Crithagra sulphuratus*	GN	1	NU	RE/SL
Cape Siskin	FRINGILLIDAE	*Crithagra totta*	GR	1	SU	RE/SL
Victorins Warbler	SYLVIIDAE	*Cryptillas victorini*	IN	0	SU	RE
Fork-tailed Drongo	DICURURIDAE	*Dicrurus adsimilis*	IN	1	NU	RE/SL
Black-backed Puffback	MALACONOTIDAE	*Dryoscopus cubla*	IN	0	NU	NO/RE
Black-shouldered Kite	ACCIPITRIDAE	*Elanus caeruleus*	CA	0	SU	NO/RE
Karoo Scrub-Robin	MUSCICAPIDAE	*Erythropygia coryphoeus*	IN	0	SU	RE
Common Waxbill	ESTRILDIDAE	*Estrilda astrild*	GR	0	SU	RE/SL
Yellow Bishop	PLOCEIDAE	*Euplectes capensis*	GN	0	SU	RE
Southern Red Bishop	PLOCEIDAE	*Euplectes orix*	GR	0	NU	RE/SL
Lanner Falcon	FALCONIDAE	*Falco biarmicus*	CA	0	NU	IA/NO/SL
Large-billed Lark	ALAUDIDAE	*Galerida magnirostris*	GN	0	SU	RE/SL
Rock Martin	HIRUNDINIDAE	*Hirundo fuligula*	IN	0	NU	RE
Southern Boubou	MALACONOTIDAE	*Laniarius ferrugineus*	IN	1	NU	RE
Common Fiscal	LANIIDAE	*Lanius collaris*	CA	0	SU	RE/SL
Cape Rock-Thrush	MUSCICAPIDAE	*Monticola rupestris*	IN	1	SU	AM/RE
Cape Wagtail	MOTACILLIDAE	*Motacilla capensis*	IN	0	NU	RE/SL
African Dusky Flycatcher	MUSCICAPIDAE	*Muscicapa adusta*	IN	0	NU	AM/RE
Malachite Sunbird	NECTARINIIDAE	*Nectarinia famosa*	NE	3	SU	AM/NO/SL
Black-bellied Starling	STURNIDAE	*Notopholia corrusca*	GN	1	NU	RE/SL
Red-winged Starling	STURNIDAE	*Onychognathus morio*	GN	1	SU	RE/SL
Black-headed Oriole	ORIOLIDAE	*Oriolus larvatus*	IN	1	NU	RE/SL
Southern Grey-headed Sparrow	PASSERIDAE	*Passer diffusus*	GN	1	NU	RE/SL
Green Wood-Hoopoe	PHOENICULIDAE	*Phoeniculus purpureus*	IN	0	NU	RE
Terrestrial Brownbul	PYCNONOTIDAE	*Phyllastrephus terrestris*	IN	1	NU	RE
Spur-winged Goose	ANATIDAE	*Plectropterus gambensis*	GN	0	NU	NO
Cape Weaver	PLOCEIDAE	*Ploceus capensis*	GN	1	SU	RE/SL
Karoo Prinia	CISTICOLIDAE	*Prinia maculosa*	IN	0	SU	RE/SL
Cape Sugarbird	PROMEROPIDAE	*Promerops cafer*	NE	3	SU	NO/RE
Black Saw-wing	HIRUNDINIDAE	*Psalidoprocne holomelaena*	IN	0	NU	IA
Red-necked Spurfowl	PHASIANIDAE	*Pternistis afer*	GN	0	SU	RE
Cape Spurfowl	PHASIANIDAE	*Pternistis capensis*	GN	0	SU	RE
Cape Bulbul	PYCNONOTIDAE	*Pycnonotus capensis*	FR	1	SU	NO/RE/SL
African Stonechat	MUSCICAPIDAE	*Saxicola torquatus*	IN	0	SU	AM/RE
Cape Canary	FRINGILLIDAE	*Serinus canicollis*	GR	0	SU	RE/SL
Cape Grassbird	SYLVIIDAE	*Sphenoeacus afer*	IN	0	SU	RE
Cape Turtle-Dove	COLUMBIDAE	*Streptopelia capicola*	GR	0	NU	RE/SL
Red-eyed Dove	COLUMBIDAE	*Streptopelia semitorquata*	GR	0	NU	RE/SL
Laughing Dove	COLUMBIDAE	*Streptopelia senegalensis*	GR	0	NU	RE/SL
Knysna Turaco	MUSOPHAGIDAE	*Tauraco corythaix*	FR	0	NU	RE/SL
Bokmakierie	MALACONOTIDAE	*Telophorus zeylonus*	CA	0	SU	AM/RE

African Paradise-Flycatcher	MONARCHIDAE	*Terpsiphone viridis*	IN	0	NU	IA
African Sacred Ibis	THRESKIORNITHIDAE	*Threskiornis aethiopicus*	GN	0	NU	NO/RE/SL
Olive Thrush	MUSCICAPIDAE	*Turdus olivaceus*	GN	0	SU	AM/RE
Tambourine Dove	COLUMBIDAE	*Turtur tympanistria*	GR	0	NU	AL/RE
Pin-tailed Whydah	VIDUIDAE	*Vidua macroura*	GR	0	NU	NO/RE
Cape White-eye	ZOSTEROPIDAE	*Zosterops capensis*	GN	2	SU	AM/RE

CHAPTER 5 – CUMULATIVE DISCUSSION

5.1 INTRODUCTION

The investigations that were run and presented in the previous two chapters yielded findings that have practical and scientific implications. This is appropriate considering the field of study into which this thesis fits; namely conservation ecology. The ecological system in which the study was conducted is as complex as it is unique, including a variety of ecological patterns and processes together with those associated with the human land-uses that fragment the system. Effective conservation of this system relies not only on the generation of scientific knowledge concerning the needs of biological communities, but also on the feasible integration of this knowledge into human land-use and management agendas. In this chapter I present the notable findings of this thesis in a way that is useful to local management and to management of similar ecological systems elsewhere. The contribution made by these findings to the broader theory concerning habitat fragmentation is also addressed.

This study was concerned with the response of two broadly different biological communities to fragmentation effects in South Outeniqua Sandstone Fynbos habitat. Vegetation and avifaunal communities were selected because they differ in terms of life-span, motility and successional cycles. Fynbos vegetation communities have exceptionally high levels of diversity which are dependent on a consistent fire-return interval (Kruger & Bigalke, 1984; Keeley, 1986; Bond et al., 1988; van Wilgen et al., 1992). Therefore these communities develop through post-fire regeneration cycles. Fynbos birds are less diverse than fynbos vegetation, yet they play an important role as plant pollinators (Bond, 1994; Pauw & Louw, 2012; Chalmandrier et al., 2013) and their motility allows them to act effectively in this regard.

The main findings of this study include an increased understanding of:

- the nature, the stability and the ecological drivers involved in the response of vegetation species to the area constraints of insular fynbos habitats;
- the role of the surrounding matrix in shaping vegetation community dynamics;
- the response of insular fynbos bird communities to indirect area-related pressures, such as vegetation quality and post-fire vegetation age;
- the existence and magnitude of extinction debt in the fynbos vegetation community but not in the avifaunal community;
- the resilience of avifaunal connectivity to the effects of the surrounding matrix.

5.2 MAIN FINDINGS

5.2.1 Vegetation species-area relationships

I investigated the persistence of the fynbos plant species-area relationship as found by Bond et al. (1988) over 24 years. The species-area relationship that was observed in the initial study was attributed to an assumed relationship between patch area and fire frequency in the natural fynbos islands (Pickett & Thompson, 1978; Bond et al., 1988). Smaller islands were supposed to receive lightning or wind-spread fire less frequently than required by local vegetation and so experience more local extinctions than larger islands. Using fire history data, I confirmed that fire has been less frequent in small insular habitats than in large insular or connected habitats of South Outeniqua Sandstone Fynbos (see Chapter 3, section 3.1). Analysis of recent community data revealed that the vegetation species-area relationship has not changed in the natural islands over 24 years, which

indicates that these habitat islands are relatively stable. Because the fynbos vegetation on the natural islands is effectively isolated by the Southern-Afrotemperate Forest matrix (Bond et al., 1988; Mucina & Geldenhuys, 2006), very little immigration can occur (see Chapter 3, Section 4 and Section 2.5 in this chapter) and thus the species-area relationship is determined by extinction alone. Because the natural islands have persisted since the early Holocene and their vegetation richness appears to be stable, I speculate that the current level of species richness is representative of communities that are fully relaxed with respect to area-related extinctions. Thus, in the absence of any area-independent extinctions that may occur, the vegetation of these islands may be thought of as being at equilibrium. Because area-independent extinctions do occur and insular communities are exposed to more pressures than those assumed by equilibrium island biogeography theory, this equilibrium should rather be thought of a quasi-equilibrium state (see Chapter 2, Section 3.7 and Chapter 3, Section 1). This state may be stable for a medium-term interval (as in Chapter 1) yet will ultimately drop so low that most fynbos species are lost or a community shift to forest-typical species will occur. This may have been the case in the smallest natural island that was studied in 1988 (see Chapter 3, Section 4 and Section 2.2 of this chapter). It is at this point of community shift, from fire-dependent fynbos to successional forest development that future studies can investigate the varying applicability of different ecological models, such as equilibrium, non-equilibrium and neutral theory, to these contrasting communities.

Management of these natural fynbos islands should consider the natural fire-return interval that corresponds with each island's size and location. A general shift towards shorter fire-return intervals has been observed across the Fynbos Biome and has been attributed to changing climatic conditions (Forsyth & van Wilgen, 2008; Wilson et al., 2010; Kraaij et al., 2012a, 2013). The results of this study and those of Bond et al. (1988) should be used in conjunction with the findings of Geldenhuys (1994) which consider the effect of island position on its fire-return interval, in order to decide on an appropriate natural fire return interval for each fynbos island. This may be a topic of future investigation. Prescribed burns may be considered in cases where the natural spread of fire from neighbouring fynbos areas on bergwinds has been intercepted by fire-suppressive human land-uses such as farmland. This should only be done within the constraints of the unique natural fire-return interval calculated for the individual islands as mentioned above.

5.2.2 Potential for vegetation community shift

The sudden shift of the natural island, "NI00" from fynbos-typical vegetation to forest vegetation after thousands of years (see Chapter 3, Section 4) may be the result of local area-independent extinctions, as discussed in the previous section. Various patterns and processes that may result in vegetation community shifts were observed in the natural islands and artificial fragments. I found a positive association between frugivorous birds and forest-typical plants and some invasive alien plants (see Chapter 4, Section 4.4) as recorded by Phillips (1927). I also found that the nature of the matrix that surrounds an insular fynbos habitat determines the type of invasive species that will be introduced to the fynbos community at the habitat edge (see Chapter 3, Section 4 and Chapter 4, Section 4.4). The role of Coral Fern – *Gleichenia polypodioides* – in shaping the insular fynbos communities is poorly understood, but its presence in the natural islands does seem to be associated with reduced fynbos species richness (see Chapter 3, Section 4). Despite these observations there is no empirical evidence that these processes result in real vegetation community shift in the fynbos islands or fragments. Future research should build on the findings and observation of this study in order to gain a better understanding of the ecological dimensions of Coral Fern in isolated fynbos habitats. Forest-typical plants that colonise the natural islands should not influence the fynbos vegetation community provided that the natural fire-return interval is consistent. An over-extended fire-return interval may

give forest-typical species enough time to become established. Forest plants are generally less flammable than the fire adapted fynbos plants (van Wilgen et al., 1990; Bond & Midgley, 1995) and therefore a community shift such as this could result in even less fire in a natural island and further local vegetation extinctions. It is certain that the occurrence of Coral Fern and the inclusion of ornithochorous forest plants to fynbos islands are natural processes and thus, under the correct fire-return interval, neither of these should be of concern to conservation management. The inclusion of ornithochorous alien plant species into fynbos islands and fragments and the spread of invasive alien plants from the surrounding matrix will however have likely implications for the persistence of fynbos communities in these habitats. Invasive alien plants are a major threat to fynbos vegetation (Cowling et al., 1976; Richardson et al., 1989; Richardson & Cowling, 1992; Holmes & Cowling, 1997a, 1997b) and affect local vegetation communities through competition and by altering the natural disturbance regime; fire-return interval, fire season and fire intensity (van Wilgen & Richardson, 1985; Brooks et al., 2004; van Wilgen, 2009; Kraaij & van Wilgen, 2011). I recommend the active removal and continued control of such species from within and around isolated fynbos habitats.

5.2.3 Avifaunal species-area relationships

I investigated the presence and nature of a bird species-area relationship in the natural islands in Chapter 4 and found that a relationship does exist and that it is similar to that of the vegetation community. The avifaunal community was less species rich than the vegetation community in the natural islands which reflects the differences in the species pools of each taxon; fynbos-typical birds are far less diverse than fynbos-typical plants as was seen in the mainland communities (see Chapter 4, Section 4.1). I also found that fynbos-typical birds in the natural islands are sensitive to post-fire vegetation age (see Chapter 4, Section 4.3) which agrees with recent findings elsewhere in the Fynbos Biome (Chalmandrier et al., 2013). Previous researchers (Lees & Peres, 2006) have found fynbos-typical birds to respond to habitat quality before habitat area in isolated communities. It is likely that the observed bird species-area relationship is in fact an indirect response to some degree; birds may be responding more directly to the improved habitat quality that is associated with larger natural islands that receive a closer-to-optimal fire-return interval (see Chapter 3, Section 4).

5.2.4 Post-fire vegetation age

Fynbos-typical birds – nectarivores in particular – play an important role in plant-pollinator mutualisms in the fynbos ecosystems (Bond, 1994; Pauw & Louw, 2012; Chalmandrier et al., 2013). Thus their response to the constraints of isolated habitats can indirectly affect vegetation communities in the natural islands and the artificial fragments. Because fynbos-typical birds are sensitive to the quality of the vegetation habitat, the appropriate management of the vegetation community in the natural islands and the artificial fragments has ecological importance. Although I found nectarivorous birds in the artificial fragments to use fynbos vegetation that is less than 10 years old, the results from the mainland habitats show that nectarivore preference is for mature, flowering vegetation that is not yet moribund (see Chapter 4, Section 4.3). A general trend of shortened fire-return intervals has been observed throughout the Fynbos Biome (Forsyth & van Wilgen, 2008; Southey, 2009; Kraaij et al., 2012a, 2012b) meaning that less high quality habitat will be available to fynbos-typical birds. Chalmandrier et al. (2013) suggested that extensive areas of fynbos should be block-burned, with individual areas being burnt at different times or years in order to create a mosaic of differently aged vegetation, thus ensuring some usable habitat for birds. However, the maintenance of a burn mosaic such as this may be difficult in large fynbos areas where fire typically spreads extensively and where there are relatively many ignition sources. The artificial fragments are often isolated from this spread of wildfire by their various matrix types. Invasive alien vegetation may act as a fire ‘super-conduit’

(Franklin & Forman, 1987; Kupfer et al., 2006), but farmland and well managed plantations with effective fire-breaks may contribute to a lower fire frequency in the fragments than in the mainland areas. The difficulties associated with conducting prescribed burns in small fragments surrounded by human land uses have been mentioned in other studies (see van Wilgen et al., 1992). If these hurdles can be overcome then the artificial fynbos fragments which are isolated from the spread of wildfire, natural or accidental, may present an opportunity to effectively develop a mosaic of differently aged fynbos habitats similar to that suggested by Chalmandrier et al. (2013). Under the correct burn schedule and fire return interval, artificial fragments will provide resource refugia for fynbos avifauna.

Another aspect that is typical of the majority of the artificial fragments is their private land ownership. Private land is typically less accessible to the public and is bordered or bisected by fewer public roads by nature of its tenure. It seems reasonable to assume that artificial fragments on private land will thus receive relatively few 'accidental' fires of anthropogenic origin, meaning that a prescribed fire-return interval may be manageable in these fragments. The artificial fragments are often areas of unproductive land that cannot be used for agriculture or silviculture (personal observation). There is potential for privately owned fragments such as these to be used in ecological stewardship programmes. Considering that most of the artificial fragments are situated on private land, the use of a stewardship programme may be more cost-effective than purchasing available fragments or land for conservation. In order that artificial fragments may function as resource refugia for avifauna, prescribed fire return intervals should be coordinated between fragments within a particular region. There is potential for this coordination to be synchronised with the fire management plans of local fire protection units. Long-term monitoring of the avifauna and vegetation communities in the artificial fragments and in the natural fynbos configurations will provide the information needed to assess the effectiveness of the proposed conservation arrangements. The advocacy of specific land tenure systems is beyond the scope of this study and thus the proposed actions must be seen as suggestions that require further investigation. Future research should also investigate effective and safe methods of prescribed burning in artificial fragments that are surrounded by human land uses. This may require an investigation into 'optimal' fire-return intervals which acknowledge the requirements of local vegetation and avifaunal communities together with the preferences of anthropogenic land uses that border the fragments.

5.2.5 Connectivity

Motility is a fundamental difference between the two groups of taxa used in this study. Although many plant species are characterised by long-distance dispersal of seeds, the ability of birds to actively migrate in response to changing conditions and resource availability makes them generally more mobile than plants. Bond et al. (1988) found that the dispersal of seeds from fynbos-typical plants is confined to the boundaries of the habitat patch, thus the rate of migration in the natural islands and, most likely, in the artificial fragments is effectively zero. The results of Chapter 4 (Section 4.2) indicate that the local migration of fynbos typical birds between the natural islands, artificial fragments and the mainland is not restricted by isolation or the nature of the particular matrix that surrounds a fynbos habitat. Nectarivores, which function as important vectors of plant genetic material in the form of pollen, seem to have suffered small loss of connectivity in any of the three South Outeniqua Sandstone Fynbos habitat configurations. Only Cape Sugarbirds (*Promerops cafer*) seem to experience reduced connectivity in the isolated habitat configurations. Although Cape Sugarbirds have been found to migrate long distances within the Fynbos Biome they seldom choose to leave areas of fynbos habitat (Hockey et al., 2005). However, the absence of Sugarbirds from these habitats could also be the consequence of some other biological preference of the species. As

mentioned in Chapter 4, these findings of connectivity are drawn from the presence or absence of bird species in habitat patches of varying isolation distance and types of surrounding matrix. Further research could use empirical evidence of species dispersal in order to verify these results for individual species, such as the Cape Sugarbird; however the presence or absence data that were used in this study provide sufficient evidence that fynbos-typical birds generally do migrate to isolated fynbos habitats embedded in human modified landscapes.

The persistence of avifaunal migration between artificial fragments, natural islands and the mainland has important consequences that complement the use of the artificial fragments as resource refugia for fynbos-typical birds. It is likely that birds will migrate between fragments that are managed so that resources become available to birds in different areas at different stages, as suggested in the previous section.

5.2.6 Extinction debt in the artificial fragments

By comparing the slope of the stable vegetation species-area relationship that exists in the natural islands to that in the mainland fynbos areas I was able to determine the magnitude of area-based local extinctions in isolated patches of South Outeniqua Sandstone Fynbos (see Chapter 3, Section 4). The difference between the two slopes is equal to the size of the extinction debt that would have been present in the artificial fragments at their time of fragmentation (Tilman et al., 1994; Malanson, 2008; Kuussaari et al., 2009; Hylander & Ehrlén, 2013). Of course this debt is only associated with area-dependent extinctions and the vegetation communities may also lose species to area-independent pressures. Area-independent extinctions may however be minor in comparison to those represented by this extinction debt. The high significance of the vegetation species-area relationships and the dominant role of area-dependent fire-return intervals in shaping these relationships are evidence of this.

Species-area relationships showed that artificial fragment vegetation communities still hold large extinction debt (see Chapter 3, Section 4). It was expected that artificial fragment avifauna would hold greater extinction debt than the vegetation community in that birds are more motile and can thus persist at levels just below their extinction threshold as a metapopulation for longer than plants (Tilman et al., 1994; Hanski & Ovaskainen, 2002; Kuussaari et al., 2009). Artificial fragment avifauna did not exhibit a species-area relationship and I could not find evidence for an area-based extinction debt (see Chapter 4, Section 4.1). It is likely that the fynbos-typical birds in the artificial fragments are responding to area independent factors, as were the birds in the natural islands. The successful detection of extinction debt in the vegetation community using simple presence/absence species data has relevance to fragmented communities in other ecosystems. This approach is very time efficient and because it relies on relatively straightforward methods it is accessible to academics and laymen alike.

The persistence of extinction debt in fragmented communities does provide an opportunity for the conservation of species that are prone to delayed extinction (Kuussaari et al., 2009). In chapter 3, it was seen that the artificial fragment vegetation community contains many such species. The local extinction of these species can be avoided by prescribing a fire-return interval to the artificial fragments that resembles the natural fire-return interval in the mainland. This can be done through the controlled burns that have been suggested in previous sections with regard to the conservation of fynbos-typical birds. This scenario will require the active removal of invasive alien plant species that are known to threaten local vegetation (Cowling et al., 1976; Richardson et al., 1989; Richardson & Cowling, 1992; Holmes & Cowling, 1997a, 1997b) and which can modify the natural disturbance

regime of periodic fire (van Wilgen & Richardson, 1985; Brooks et al., 2004; van Wilgen, 2009; Kraaij & van Wilgen, 2011) and thus result in area-independent extinctions. It may be argued that the artificial fragments should be managed in the same manner as the natural islands and that no prescribed burning should be used. Through this approach, biological communities may result that are similar to those in the natural islands. This could be seen as the preservation of a system that does occur naturally in the area and it would be far simpler than attempting to preserve mainland species levels in the artificial fragments. An approach such as this would however be hard to justify given that the fragments support many IUCN red data listed plant species (see Appendix 5.1) and have potential to serve as resource refugia for fynbos-typical birds.

5.2.7. Application of equilibrium island biogeography theory in fynbos fragments

Natural islands and habitat fragments are similar with respect to their area and isolation constraints (Haila, 2002; Laurance, 2008). The application of equilibrium island biogeography theory in fragmentation studies has been reviewed in Chapter 2. It is apparent from the literature that this theory can be used as a framework through which to investigate the response of biological communities to certain aspects of their fragmented habitat. Fragment area and degree of isolation can usually be assessed through this framework; however the nature of the fragmented community and the nature of the surrounding matrix often have a modifying influence on these constraints (see Chapter 2, Section 3). Because the isolated vegetation communities are dispersal limited (Bond et al., 1988) there would be merit in their future examination through niche-assembly theory (Hubbell, 2001). Fragmented communities of South Outeniqua Sandstone Fynbos vegetation are however well described by island biogeography theory in that they are predominantly shaped by area-related extinctions (see Chapter 3, Section 4). It must be appreciated though, that the nature of the human-modified matrix which surrounds these communities is likely to be responsible for further, area-independent extinctions. These matrix habitats can alter disturbance regimes within fragments or even introduce novel disturbances (see Chapter 2, Section 3). In the case of South Outeniqua Sandstone Fynbos, the alteration of the natural fire regime and the introduction of invasive alien plants to the artificial fragments may drive area-independent extinctions.

The fynbos-typical birds that use South Outeniqua Sandstone Fynbos habitats respond to habitat quality which is in fact linked to habitat area in isolated fynbos patches. Birds typically vary in their mobility and thus it is likely that fragment isolation has separate effects on different species. In Chapter 4, it was apparent that Cape Sugarbirds are absent from the isolated habitats – possibly due to the influence of the surrounding matrix on the isolation of the habitats for these birds. This shows that fragmentation studies should not rely on investigation of the two main constraints acknowledged by island biogeography theory –area and isolation – alone. A more effective way of using the island biogeography framework in such research would be to consider a fragment's effective area and isolation, which will vary between species (see Chapter 2, Section 3).

The concept of the equilibrium state in fragmented communities should also be carefully considered. The area-dependent extinctions that have occurred in the natural islands have left the local plant communities at a relatively stable state of species richness (see Chapter 3). Because communities are effectively isolated from the arrival of new fynbos colonists (Bond et al., 1988), and because stochastic, area-independent extinctions are often delayed (Lande, 1993; Dennis, 2002), they resemble communities that have reached an equilibrium state. However, we know that area-independent extinctions are likely to occur in the natural islands and in the artificial fragments at some stage. Therefore this stable state may be temporary yet persistent enough to have use in fragmentation studies such as this, and should be considered a quasi-equilibrium state (see Chapter 3). Future

research should investigate whether non-fragmented fynbos communities of varying mobility and competitive ability are best investigated through the lens of dynamic equilibrium, non-equilibrium or neutral theory and whether this varies at different levels of diversity in the landscape.

5.3 CONCLUSION

The various habitat configurations that exist in South Outeniqua Sandstone Fynbos have provided useful insights into the conservation of biological communities that occupy them. In some cases these insights have application in other ecosystems that are also faced by the pressures of habitat fragmentation. This system should not only be conserved for the biological value that it holds but also for the potential that it holds to answer the future questions that may be asked about fragmented habitats. There is potential to conserve the system through various prescriptions and to ensure various outcomes. Additionally, the conservation value of fynbos remnants that persist within the largely human-modified matrix should not be overlooked.

"Igne natura renovator integra" (through fire, nature is reborn whole – alchemist phrase).

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Appendix 5.A – Inventory of nationally red-listed plant species recorded in this study. Status categories are abbreviated as: CR – critically rare; DC – population declining; EN – endangered; NT – near-threatened; RA – rare; VU – vulnerable. "Year assessed" indicates the year of most current national assessment of each species. "Typical-habitat" refers to the habitat – indigenous forest (FO) or fynbos (FY) – to which the species is generally associated. Study site codes are the same as those used throughout the study and refer to the particular areas of habitat in which the species was recorded together with the year of recording. "AF" refers to artificial fragments, "NI" refers to natural islands and "ML" refers to the mainland. All data concerning the status of these species were obtained from the South African National Biodiversity Institute (2010).

Family	Genus	Species	IUCN red list status*	Year assessed	Typical-habitat	Study-site
AQUIFOLIACEAE	*Ilex*	*mitis*	DC	2009	FO	NI048 (2012)
CELASTRACEAE	*Elaeodendron*	*croceum*	DC	2009	FO	AF015(2012)
						ML (1988)
CORNACEAE	*Curtisia*	*dentata*	NT	2008	FO	NI018 (2012)
						NI042 (2012)
						NI048 (2012)
						NI064 (2012)
						NI037 (1988)
CYATHEACEAE	*Cyathea*	*capensis*	DC	2009	FO	AF018 (2012)
DIOSCOREACEAE	*Dioscorea*	*sylvatica*	VU	2009	FO	AF010 (2012)
						ML (2012)
ERICACEAE	*Erica*	*onusta*	CR	2009	FY	ML (1988)
FABACEAE	*Aspalathus*	*bowieana*	EN	2009	FY	AF033E (2012)
FABACEAE	*Cyclopia*	*subternata*	DC	2011	FY	AF011 (2012)
						AF040 (2012)
						NI044 (2012)
						ML (1988)
FABACEAE	*Lebeckia*	*meyeriana*	EN	2009	FY	NI042 (2012)
						ML (2012)
HYPOXIDACEAE	*Hypoxis*	*hemerocallidea*	DC	2009	FY	AF010 (2012)
						AF014 (2012)
						AFQD (2012)
						AFTD (2012)
						AFTP (2012)
						AFTB (2012)
IRIDACEAE	*Gladiolus*	*sempervirens*	RA	2009	FY	ML (2012)
LAURACEAE	*Ocotea*	*bullata*	EN	2009	FO	AF011 (2012)
						NI019 (2012)
						NI064 (2012)
MYRSINACEAE	*Rapanea*	*melanophloeos*	DC	2009	FO	(2012)**
PENAEACEAE	*Penaea*	*acutifolia*	RA	2009	FY	ML (2012)
PROTEACEAE	*Leucadendron*	*conicum*	NT	2009	FY	ML (2012)
PROTEACEAE	*Leucospermum*	*glabrum*	EN	2009	FY	ML (2012)
PROTEACEAE	*Mimetes*	*pauciflorus*	VU	2009	FY	ML (2012)

*Certain categories included are recognised by the national programme and not the IUCN.
**Species recorded in most artificial fragments and natural islands, and in the mainland.